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GENETIC ALTERATIONS TO ARTIFICIAL SOILS BY EARTHWORMS

by

©

CINDY SHAW

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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IN
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....

Date October 5, 1984

Abstract

The primary objective of this study was to examine the role of earthworms in structural development. Secondary objectives included an examination of their role in decomposition and influence on soil chemistry.

A microcosm study was set up using biologically unaltered parent materials from three textural classes and earthworms from two ecological groups. After one year chemical, microbiological and X-ray diffraction analyses were performed on component parts of the microcosm and micromorphological techniques were used to study the structural development.

Lumbricus terrestris played a primary role in structural development by withdrawing litter from the surface into the soil and bringing it into intimate contact with inorganic constituents. *Octolasion tyrtaeum* and *Aporrectodea turgida*(geophages) played a secondary role by ingesting large quantities of matrix material which was physically altered and translocated, resulting in homogenization of the soil. A synergistic effect occurred where both ecological groups of earthworms co-existed.

Significant contributions to organic plasma concentrations, which bound inorganic soil constituents together, were made by all species. Where a high proportion of clays were present earthworms increased the degree of their orientation.

In the silty clay loam(SiCL) soil granular structure developed in the presence of all species of earthworms. This structure was strongly associated with high concentrations of clay-bound neutral sugars in the faecal pellets. In this soil earthworms accelerated decomposition through their ability to maintain viable populations of fungi and anaerobic bacteria. Accelerated decomposition in the presence of earthworms proved beneficial since a high proportion of extractable carbon was stabilized through intimate association with clays. Stabilization of organic carbon was attributed to a high proportion of smectite clays in the SiCL soil.

In the clay loam(CL) soil fusion of the matrix material was strongly expressed where *L.terrestris* was active alone and with the geophages. Fusion of the matrix was associated with low concentrations of clay-bound neutral sugars in the faecal material. Decomposition was accelerated by earthworms in the CL soil in a fashion similar to the SiCL soil but proved far less beneficial. A small proportion of extractable carbon was present in the clay-bound component and respiration losses of carbon were high. The poor ability of the CL soil to stabilize carbon was attributed to the low proportion of smectite clays present.

In the sandy loam(SL) soil weakly expressed granular structure developed where the geophages were active. This was associated with the highest concentrations of clay-bound neutral sugars in the faecal pellets for this soil. Fusion of the matrix occurred where *L.terrestris* was active alone and decomposition was retarded. Retarded decomposition was attributed to the inability of the earthworm to maintain viable fungal populations whereas it could in the CL and SiCL soils.

All species of earthworms enhanced the mobilization of calcium, magnesium and sodium. Losses of these elements were highest where *L.terrestris* was present since its tunnelling behavior was conducive to enhanced leaching Potassium data suggested that geophageous species may be involved in de-potassification of clay minerals.

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My gratitude felt towards my family and friends(whom I intend to get re-aquainted with) for their continued support and patience is immeasurable. May God bless their soils with earthworms that produce a favourable, granular, mull type of structure.

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1. INTRODUCTION

Numerous soil fauna are involved, to some degree, in pedological processes but earthworms are most often singled out as being uniquely important in the development of a stable, granular, mull structure. This belief has arisen mainly from the association observed between the presence of earthworms and soils having a well developed granular structure. Although it is implicit in many statements that earthworm activity alone produces granular structure, little direct evidence for this exists. The majority of studies which have led to this conclusion were conducted using soils in which earthworms had been active for a considerable length of time or a granular type of structure already existed. Under these conditions it is difficult to determine what features in the fabric can be attributed to the activity of earthworms, as opposed to those resulting from other genetic processes or the activities of other soil fauna. Thus, conflicting opinions exist regarding the role earthworms play in the genesis of humus forms. Can they, acting alone, modify the organic constituents of the soil in a manner that facilitates binding with the inorganic fraction to produce a mull type of fabric or; do they simply play a secondary role in mixing and homogenizing materials already modified, either by other soil biota or through other pedogenic processes?

The notion that the effect earthworms have on soil structure is always a positive one originates mainly from studies conducted in European ecosystems where soils, climate, vegetation, species of earthworms and their population numbers differ significantly from those found in Canada. The contrast is particularly sharp when European ecosystems are compared with the parkland and prairie regions of Canada. In these regions individuals have reported that earthworms destroyed what had previously been good granular structure in their garden soils. In correspondence to J. Thorp, A. Leahey(former head of the Dominion Soil Survey Staff of Canada) stated that soils of Alberta and Manitoba were damaged by earthworms that were introduced(Thorp, 1949). He related an experience where residents on a farm north of Edmonton observed that earthworms ruined their garden in less than two years. The earthworms turned the granular, friable structure of a Chernozemic clay soil into a sticky mass which was extremely difficult to manage. Agarwal et al.(1957) observed a similar effect where earthworms belonging to the genus *Allolobophora* destroyed the granular structure of soils having clay loam and silty clay loam textures. Thus, another conflict of opinions exists. Is the effect earthworms have on soil structure always a positive one?

The species *Lumbricus terrestris* has been used extensively by researchers for the study of earthworm-soil relationships. Information derived from these studies is often incorrectly interpreted as representative for all species of earthworms. Earthworms can be classified into ecologically distinct groups which are defined by feeding behavior and spatial distribution in the soil. The effect earthworms have on soil processes reflects how they function ecologically, yet little work has been done to demonstrate these differences in terms of soil structure development.

The mechanisms and processes which are thought to be involved in aggregate formation and stabilization have been studied for years and were summerised in a review article by Harris et al.(1966). Despite the availability of this information few efforts have been made to determine which of these processes may be influenced by earthworms to produce or stabilize soil aggregates.

Based on the foregoing conflicts of opinions and gaps in knowledge the following primary objectives were set for this study.

1. To determine if earthworms, acting alone, can produce a granular type of soil structure.
   If so;
   - a) Does the effect vary depending on the original texture of the soil?
   - b) Does the effect vary depending on the species of earthworm involved?

2. To determine if processes traditionally considered to be involved in aggregate formation and stabilization are influenced by the activities of earthworms. The processes to be examined include:
    - a) Formation of organo-clay complexes
    - b) Enhancing production of polysaccharides and/or uronic acids
    - c) Reorganization and compaction of soil material
    - d) Movement and concentration of colloidal materials
    - e) Promoting growth of microbial populations

Almost no information is available regarding earthworms and their influence on the cycling of elements, with the possible exception of Ca. For this reason, and to complement information gathered to satisfy the primary objectives, the following secondary objectives were set for this study.

1. To gather baseline information regarding earthworms and soil chemistry.
2. To gather information regarding the influence of earthworms on decomposer organisms.
3. To determine changes in soil porosity as influenced by earthworms.

In order to satisfy these objectives a microcosm study was set up under controlled environmental conditions. Unaltered parent materials from three different textural classes were packed into columns. Earthworms from different ecological groups were allowed to inhabit the columns for approximately one year. At monthly intervals grass was added to the top, and leachates were collected from the bottom of the columns.

Thin sections(32um thick) were prepared from these soils and described to meet primary objective #1 and portions of #2. The soil in each column was dissected and separated into portions affected and not affected by earthworm activity. These samples were analyzed using the appropriate methods to meet primary objective #2.

The following analyses were done to meet the requirements of the secondary objectives.

OBJ. #1: Elemental analysis of grass residues, soil samples, and leachates.

OBJ. #2: Soil samples were used to determine total microbial numbers and to obtain isolates for specific assays.

OBJ. #3: Examination of 32um thin sections.

2. LITERATURE REVIEW

2.1 Introduction

Much of our thought and understanding about earthworms and their involvement in the soil system originates from European research. This review provides an overview of the current line of thought regarding earthworms and their function in the soil system. However, these observations and conclusions apply largely to European ecosystems and species of earthworms. The basic information must be interpreted with caution due to large differences in ecosystems, approaches to land management, and the limited availability of knowledge regarding the population density, distribution and kinds of earthworms in Canada.

2.2 History of Research on Earthworms

The initial surge of interest in earthworms and their involvement in soil processes began with the work of Charles Darwin(1881). His book, Earthworms and the Formation of Vegetable Mold was met with considerable criticism. Darwin made a case for the positive influence of earthworms on enhancing the productivity of land, when the current mode of thinking was the contrary(Edwards, 1981). This attitude quickly changed and by the turn of the century earthworms were being viewed in an overwhelmingly positive light. Numerous theories were put forth regarding the influence of earthworms on a wide variety of soil physical and chemical properties (Russel,1910;Salisbury,1924;Wherry,1924). This period of interest was short lived and it was not until the mid 1950's that a resurgence of earthworm research was spearheaded by John Satchell. A solid and reputable research group was formed in England under the auspices of Satchell, including individuals such as D. Lowe, G. Heath, J. Lofty and C. Edwards. During the 1960's researchers in several other countries began making significant contributions to the study of earthworm-soil relationships including O. Graff in Germany, C. Jeanson in France, J. Van der Drift and J. Van Rhee in the Netherlands, K. Lee in New Zealand and K. Barley in Australia. Over the last decade several research groups, emphasizing an ecological approach to the study of earthworms, have emerged from Russia, New Zealand, Australia and several Scandinavian countries.

In North America the scenerio is much less positive where publications regarding earthworms can be found, but they occur intermittantly as "novelty items" and do not reflect a strong interest in the area of earthworm-soil relationships. An exception to this is the work of the Canadian, John Reynolds, who has published extensively on the ecology and taxonomy of earthworms in Canada and the United States.

2.3 Distribution and Occurrence of Species in Canada

One of the major reasons for the scant interest expressed in studying earthworms and soils at the process level in Canada is likely the distinct lack of knowledge regarding the distribution of species and population numbers which occur here. Since there is only a dearth of knowledge on this subject it has been inferred that these soil fauna are of little significance to the soil system.

The most commonly accepted theory regarding the distribution of earthworms in North America is that during the Quaternary Period most species indigenous to glaciated North America were exterminated(Reynolds,1977). Those species with which we are most familiar in Canada are thought to have been introduced by man through colonizers from other continents or from southern refugia (Reynolds,1977). Reynolds(1977) stated that of 19 Ontario species of earthworms only 2 are native to North America. If one were to accept this theory, it would be logical to expect that the distribution of earthworms in Canada largely follows the pattern of settlement of the country by human occupation. This seems to be the case as earthworms do commonly occur in populated areas whereas in remote areas it is considered unusual to find them.

Although virtually nothing is known regarding earthworm population numbers in Canada, Reynolds(1977) publication The Earthworms of Ontario provides considerably detailed information regarding species distribution in Ontario along with general information on distribution in North America. Of the 19 species described by Reynolds(1977) the existence of only 6 has been documented in the prairie provinces. In fact, some of the species used in this study are the first documented evidence for their existence in Alberta.

2.4 Taxonomy and Ecological Classification of Earthworms

Taxonomically earthworms belong to the phylum Annelida and order Oligochaeta. The majority of specimens whose existence is documented in Canada belong to the family Lumbricidae, while some occur in the family Sparganophilidae(Reynolds,1977). Recently specimens belonging to the family Megascolicidae were found on Vancouver Island(McKey-Fender and Fender,1982).

Considerable confusion exists regarding taxonomy at the species level. For example, Reynolds(1977) described the species *Octolasion tyrtaeum* and lists over 10 different species names which have been assigned to this earthworm in research articles. This type of confusion makes it difficult to collate research on any one species in order to understand its function in the ecosystem.

In order to circumvent this problem several individuals have developed ecological classification systems. This enables one to study earthworms as ecologically functional groups where knowledge of individual species is not essential for interpreting information (Gates, 1961;Bouche, 1972;Norstrom and Rundgren, 1973;Perel, 1977).

Strong similarities exist between most of these ecological classification systems which are largely based on feeding habits and spatial distribution of the earthworms. One such system described by Perel(1977) is outlined as follows;

TYPE I:Feeding on or at the soil surface consuming only slightly decomposed plant residues.
    GROUP 1:Soil surface or litter dwellers
    GROUP 2:Topsoil and litter dwellers
    GROUP 3:Deep hole-makers

TYPE II:Feeding on decaying plant matter dispersed in mineral soil layers.
    GROUP 1:Top-soil dwellers
    GROUP 2:Middle mineral strata inhabitants
    GROUP 3:Deep hole boring species

Perel(1977) referred to the Type I and II feeders as "morph-ecological types" as their adaptation to different feeding habits is reflected in distinct morphologies. Type II feeders are characteristically pigmentless, less motile with primitive bundle-like muscle fibres, and the typhlosole is intensively folded providing a large surface area for nutrient absorption from finely divided organic matter. Type I feeders are commonly pigmented, highly mobile having complex muscle fibre types, and the typhlosole is small with few or no folds.

Classification at the group level is based on vertical distribution in the soil which reflects the feeding behavior and adaptation to surviving adverse moisture or temperature conditions. For example, deep-hole borers are adapted to well drained soils where periodic drying occurs, since they can escape to depth(150+ cm) and diapause. On the other hand *Octolasion lacteum*, a mineral soil layer dweller, has a weak ability to diapause but is well adapted to sites which are permanently moist or even periodically flooded, having a well-developed subcutaneous net of blood vessels and a high concentration of haemoglobin(Perel, 1977).

With the current confusion regarding taxonomy of earthworms at the species level, it is apparent that an ecological classification system such as that developed by Perel(1977) has far more utilitarian value in terms of synthesizing and applying information. However, this does not diminish the value of a traditional taxonomic system which should ultimately expedite the process of applying information when a species is identified and placed in an ecological group whose function in the ecosystem is understood.

2.5 The Ecology of Earthworms

Numerous ecological studies have been carried out in an attempt to determine what environmental factors dictate the distribution and population numbers of earthworm species(Nordstrom and Rundgren, 1974;Rozen, 1980;Ljundstrom et al, 1973; Heitor, 1969). Conflicting observations resulting from these studies only serve to emphasize the fact that one can not view the ecology of earthworms in an oversimplified vein. Earthworms can not be grouped into a singular taxonomical unit whose members all function in a similar manner within the ecosystem. In order to sort out the complex interactions of earthworms with each other, with other biota in the ecosystem, and with their environment, studies must be carried out at the species, or at least at an ecologically functional group, level. It must be recognized that ecological niches exist for different species or groups of species of earthworms.

The following review will discuss the most popular viewpoints regarding earthworm ecology while providing examples to illustrate that these generalizations must be interpreted with caution.

The basic requirements of earthworms were listed by Lee(1959) as follows;

1. Adequate and suitable food supply
2. Adequate moisture assuming 1. is met
3. Adequate dissolved O_2

4. Protection from light
5. Favourable temperature regime
6. Suitable pH

Some disagreement exists as to the relative importance of these factors. Logically one may assume that depending on the species of earthworm and the ecosystem under consideration the relative importance of environmental factors would shift.

Although Lee(1959) included protection from light and the presence of adequate dissolved O_2 as important requirements for earthworms, they will not be discussed in detail. Considering that earthworms are basically subsurface dwellers which are relatively mobile they could easily escape any damage from exposure to light through avoidance behavior. Although the lack of adequate dissolved O_2 may explain the absence of earthworms on a localized basis this notion may be applied to any biological entity dependent on aerobic respiration for existance, therefore this factor should not be considered uniquely important in controlling the distribution and activity of earthworms.

Thus, the following discussion will focus on the remaining factors listed by Lee(1959). I have chosen to discuss these factors by dividing them into two broad categories. The first, earthworm nutrition, will be discussed in the traditional sense of litter providing an ultimate energy source for the earthworms, but will also include a discussion of earthworms as grazers as opposed to detritivores. The second category will include a discussion of soil properties, both physical and chemical, which are considered to influence earthworm activity and distribution. Factors outlined by Lee(1959) such as moisture, temperature and pH are included in this section.

2.5.1 Nutritional Requirements and Feeding Habits of Earthworms

In order to support a viable earthworm population an adequate(quantity) and suitable(quality) food supply must be available(Lee, 1959). Since the feeding preferences of earthworms have not been established the quantitative aspects of food supply will not be discussed. The following discussion will lay out the current status of knowledge regarding feeding preferences.

Miles(1963) stated,

> "It is clear that some of the effects produced in soil both with regard to composition and structure are consequences of the feeding habits and nutrition requirements of earthworms"

Despite this concept, virtually nothing is known regarding the nutritional requirements of earthworms. Because earthworms obviously ingest organic materials(leaf litter, grass etc.) most feeding experiments, although limited in themselves, have been oriented towards studying the selection of different types of leaf litter(Satchell et al., 1967;Gast, 1937;Edwards and Heath,1963;Mangold,1951).

These studies were conducted using one species, *Lumbricus terrestris*, and yet few consistencies in selection were observed. It can not be overemphasized that these feeding studies utilized only one species of earthworm. *L. terrestris* is widely popular for earthworm research since it is readily available and easy to handle and maintain. It is particularly attractive for feeding studies as it characteristically withdraws litter from the surface into the ground(Type I - Group 3 - Perel, 1977). Because of this unique feeding habit the job of the researcher is simplified as food selection can be monitored easily. It must be recognized that this species occupies a unique ecological niche and data collected regarding feeding must be considered to apply only to that species or at best, only to surface feeding, deep burrowing earthworms.

Gast(1937) studied *L. terrestris* and established the following levels of preference.

Most preferred	- large toothed aspen, white ash, basswood
Secondary	- sugar maple, red maple
Refused	- oak

He attributed these preferences to mineral content of the leaves stating the earthworms preferred those species able to cycle basic nutrients(K, Ca) from the depths of the soil. Mangold(1951) coated boiled pine needles with a gelatinous substance containing ground up material from different leaves. He established the following order of preferences.

Fresh - beech, maple, oak, horsechestnut,
lime, willow, false accaria
Decayed - willow, false accaria, oak, lime,
beech, maple, horsechestnut

He attributed the sequence of preference to the accumulation of polyphenols.

In 1963 Edwards and Heath found the stage of leaf maturity determined its succeptability to decomposition when it reached the forest floor. They stated it was important that the leaves abscised before the accumulation of polyphenols occurred since this resulted in the precipitation of proteins making leaves less digestible. They found that oak decomposed faster than beech. Leaves that were unacceptable to earthworms were also not decomposed by bacteria or fungi.

A comparison of these studies regarding the palatability of litter to earthworms points out noticeable discrepancies. For this reason Satchell and Lowe(1967) embarked on a comprehensive palatability study with *L. terrestris*. They stated that in the vegetation preference studies conducted up to that time, little work had been done on the contents or physical properties of litter. It was thought that a study of these properties might provide some clue as to why one type of vegetation was preferred over another. They conducted numerous tests on the physical and chemical properties of vegetation and generally concluded that physical properties such as thickness, toughness and water content, had little influence on the preferences of *L. terrestris*. The chemical tests resulted in better correlations. The analyses can briefly be summerised as follows.

1. A correlation existed between nitrogen content and preference but the earthworms demonstrated no sensory detection of amino acids. Also, alder was not highly preferred even though it is a known nitrogen fixer.
2. A broad correlation was established between sugar content and palatability, but again the earthworms had no sensory detection for the presence of sugars.
3. A very high negative correlation was found between initial polyphenolic content and palatability and palatability increased after polyphenols were weathered out. The exception to this was alder which was highly palatabe relative to its polyphenolic content.
4. A strong negative correlation existed between palatability and tannin content but the authors failed to explain why ten species remained unpalatable after tannins were removed from the vegetation.

From their studies Satchell and Lowe(1967) indicated that tannins were the most important chemical substance rendering vegetation unpalatable to earthworms.The general conclusion was that the factors controlling food selection remained unknown. They did observe that as litter became increasingly decomposed it was preferentially selected and attributed this to the breakdown and leaching of polyphenols. Subsequent tests in this regard produced inconsistant results. Cooke et al.(1980) thought this observation may have resulted from the earthworms preference for the agents of decomposition, rather than the predisposed plant material itself. Using control discs plus those cultured with *Mucor hiemales, Penicillium sp. and Pseudomonas fluorescens,* they found fungi were preferred over the bacterium, which was selected over the control discs. They speculated the preference was due to the higher nitrogen content of the fungi.

The following observations provide further support for the concept that earthworms metabolize microorganisms, rather than plant material, to satisfy their nutrient and energy requirements.

1. Decreases in microbial numbers in the intestine of earthworms(Dawson, 1947;Day, 1950;Nekrasova et al.,1976;Atlavinyte et al.,1973a).
2. The majority of plant detritus passed through the gut without extensive degradation(Pierce, 1978;Parle, 1963;

Nielson, 1962).

3. Earthworms lack the enzymic complex necessary for the breakdown of complex carbohydrates(Nielson, 1962).
4. C:N ratios of casts sometimes are greater than the surrounding soil(Syers et al., 1979;Lunt et al., 1944;Watanabe, 1975).
5. Low carbon assimilation rates for ingested materials(Bolton and Phillipson, 1976).
6. Occurance of fatty acids in lipid fractions of earthworms, which were most likely assimilated from ingestion of soil microorganisms or other fauna, rather than plant materials in which they were not detected(Hansen et al.,1975).

Although these points support the concept that earthworms metabolize microorganisms sufficient conflicting data exist to indicate further research is needed in this area (Parle, 1963b;Day, 1950; Nielson, 1962; Bolton et al., 1976). Parle(1963b) found that gut bacteria and actinomycetes increased logarithmically through the gut of *L. terrestris*. He was not certain why this happened but suggested it may be the presence of sugars released from enzymatic degradation of organic matter increased accessability to organic matter after comminution by the earthworm. Day(1950) found no consistant increase or decrease in numbers of microorganisms in the gut of earthworms. However, his work was contested by

Parle(1963b) and Edwards et al.(1977) because the earthworms were placed in compacted soil forcing them to establish burrows first. This resulted in abnormal feeding, where the earthworms ingested proportionally higher amounts of mineral soil. Therefore estimates of microbial numbers approximated those of the soil itself. Erroneous results may be obtained when earthworms are sampled during a season when they are not actively feeding. Bassalik in Dawson(1947) found that numbers of 11/10/52(x10^{6}) organisms per gram occured in the intestine/casts/soil at $^{-}3$° C, but 20/148/64(x10^{6}) at 16°C. Hansen et al.(1974) found 13.3% fatty acids in earthworms in the spring and only 3% during the winter. They attributed this to the greater feeding on microorganisms during the spring period.

Bolton et al.(1976) felt that the highly comminuted nature of the gut contents in *Allolobophora caliginosa* indicated that plant detritus, rather than microorganisms, was the main source of food for these earthworms. Because their work was not accompanied by microbial experiments this conclusion appears unsubstantiated. The fact that *A. caliginosa* prefers to feed on highly decomposed organic matter may in fact indicate a greater preference for the decomposing organisms.

Although it was stated by Nielson(1962) that earthworms do not possess the digestive enzymes to break down complex materials, some enzymes which could aid in this function have been detected in gut extracts(Table 1). Some dispute

Table 1:Enzyme activity detected in the gut and of isolates from the gut of earthworms

Enzyme	Earthworm	Reference
Cellulase	*Dendrobaeina octaedra*	Nielson,1962
	17 species	Tracy,1951
	Nicodrilus longus	Loquet et al.,1977
	N. nocturnus	
	Pheretima sp.	Khambata et al.,1957
	Dichogaster bolaui	Mishra et al.,1980
	Octolasium lacteum	Kozlovskaja,1969
	Lumbricus rubellus	
	Eisenia nordenskioldi	
	Eisenia sp.	Arthur,1965
	L. terrestris	Parle,1963b
Chitinase	*L. terrestris*	Parle,1963b
	12 species	Tracy,1951
	Dendrobaena octaedra	Nielson,1962
Protease	*L. terrestris*	Laverack,1965
	Allolobophora sp.	
	Pheretima sp.	
	Octochaetona surensis	Mishra et al.,1980
	Drawinda calebi	
	Lampito mauritii	
	L. terrestris	Robertson,1939
Amylase	*O. surensis*	Mishra et al.,1980
	D. calebi	
	L. mauritii	
	L. terrestris	Robertson,1939
	Dendrobaena octaedra	Nielson,1962
	A. caliginosa	
Urease	*Lampito mauritii*	Mishra et al.,1980
	Drawinda calebi	
Oxalase	*Pheretima sp.*	Khambata and Bhat (1953,1955,1957)
	Tsuga heterophylla	Cromack et al.,1977
	Lumbricus rubellus	
Lipase	*L. rubellus*	Hansen et al.,1974
	A. caliginosa	
	L. terrestris	Robertson,1939

exists regarding the source of these enzymes. That is, are they secreted by the earthworm itself, extracted from ingested microbial and plant material, or are they the product of some indigenous gut microflora or fauna? The work of Parle(1963b) substantiated reasonably well that cellulase was produced by the earthworm itself, while chitinase was produced by the earthworm and gut microorganisms. Mishra et al.(1980) worked solely with microorganisms isolated from the gut, so it appears these enzymes were produced by the gut microbes. Their work did not confirm that the organisms studied were indigenous to the gut. Much disagreement exists on this point although little work has been done to definitively prove whether or not microbes unique to the gut of the earthworm exist.

Three papers relevant to the topic of gut organisms provide evidence that earthworms may have indigenous protozoa or at least that protozoa are essential to their nutrition. Dixon(1975) described three common genera of the Astomatida ciliates from the gut of British earthworms. He stated that astomatous ciliates occur in many invertebrates but are most common in annelids and are very abundant in oligochaetes. Pierce et al.(1980) tested the effect of alimentary fluids from *L. terrestris* on the ciliate *Colpidium canpylum*. They found the mid gut fluid(the region of highest enzyme concentrations) was extremely hostile to these organisms; halting their activity and in some cases disintegrating them. Yet, 78 specimens of astomatous ciliates were found living in this hostile gut fluid and demonstrated no abnormal activity. They concluded that these protozoa could not be considered a mere extension of soil and water inhabiting ciliates, since they had developed a unique physiology in order to survive the alimentary fluid. Miles(1963) cultivated populations of *Eisenia foetida* under sterile conditions. These earthworms were placed in containers inoculated with bacteria and fungi, and bacteria, fungi and protozoa. Earthworms having the protozoa grew significantly larger than those without and were the only ones to mature.

Digestive fluids of earthworms not only affect ciliates, but also bacteria and fungi, in different ways. Aichberger (in Day,1950) found organisms that did not possess a firm outer coating, such as desmids, blue-green algae, yeast and rhizopods, were present in the crop and gizzard but significantly decreased in number in the intestine. Day(1950) found that *Serratia marcensens*, a non-sporing bacterium, was present in the pharynx, but completely absent from the crop and intestine. *Bacillus cereus* var. *mycordes*, a sporing bacterium was reduced in numbers but still persisted. The spore forming bacteria *B. idosus* and *B. cereus* were also found to be higher in number in the casts of *Pheretima* sp.(Edwards et al., 1977). Day(1950) attributed this to earthworms assimilating the vegetative cells but not the spores. Nielson(1962) lent further credance to this observation when he found that trehalase activity was non-existant in the gut of three earthworm species. He stated that trehalose constitutes a large percentage of material in fungal spores. If earthworms do not have the enzymes necessary to degrade the spores they will persist while passing through the gut.

The foregoing evidence indicates that protozoa and bacteria are important in the nutrition of earthworms. Symbiotic bacteria and protozoa are known to have an important function in the breakdown of plant materials in other animals(cow,shipworm) and it is likely they serve a similar function in earthworms.

The previous discussion has emphasized the current lack of consistent information regarding the nutrient requirements and feeding habits of earthworms. These are obviously more complex than the simple ingestion of plant detritus. Recent work indicates that either microorganisms are in themselves a primary nutrient source for earthworms, or they act, possibly in association with other gut organisms, in the decomposition of plant tissues to release basic constituents for assimilation by earthworms.

As previously stated, an understanding of the feeding habits and nutrient requirements of earthworms is important in gaining an understanding of their influence on soil processes and behaviour in their environment. The traditional view that earthworms merely ingest, comminute, and expel plant detritus in a physically altered form should be re-examined. In addition, large differences in feeding habits and nutritional requirements between species or "morph-ecological groups" should be recognized to allow for valid interpretation of the function and activity of earthworms in their environment.

2.5.2 Soil Properties

Soil moisture, temperature and reaction are most commonly cited as factors controlling the distribution of earthworms(Reynolds and Jordan, 1975). Edwards and Lofty(1977) emphasized that soil properties, such as those listed above, in addition to inorganic salts, aeration and texture are important in determining the horizontal distribution of earthworms while seasonal variations in moisture and temperature play a more important role in determining vertical distribution. The latter portion of this statement may, in part, be true but recent studies have placed greater emphasis on considering the ecological niche as a major determinant for vertical distribution(Phillipson et al., 1976;Ljundstrom et al.,1973). The following discussion will focus on those soil properties which are commonly cited in controlling earthworm distribution although some reference will be made to ecological interpretations.

2.5.2.1 Soil Moisture

Given the availability of an adequate and suitable food source, adequate soil moisture becomes the most important factor determining the survival of earthworms (Abbott et al.,1980;Reynolds et al.,1975). This is particularly true for earthworms, as opposed to many other soil organisms. Earthworms lack a mechanism to conserve water and are dependent on the diffusion of water soluble gases through the body wall for respiration(Lee, 1959;Reynolds et al.,1975). In nature earthworms can avoid fatal desiccation either through diapause(facultative or obligatory) or through retreat to the subsoil(Roots, 1956).

Some researchers have been able to relate the mechanism used by a particular species to deal with desiccation, to its ecological niche. For example, Roots(1956) found *A. chlorotica* had a wide tolerance to fluctuations in soil moisture and interpreted this as an adaptation of surface dwelling species which are frequently subjected to such variations. Conversely she found *L. terrestris* was less tolerant to extremes in soil moisture, but because of its greater mobility and ability to burrow to great depths it can escape from adverse soil moisture conditions. Similarly Ljundstrom et al.(1973) observed in Argentina that the species *Eukerria halophila* had a low tolerance to desiccation. In the field its distribution was restricted to water-logged soils with moisture contents ranging from 60-62%(w/w).

In reference to population dynamics it appears that fluctuations in moisture have their greatest influence on population structure and thus an indirect influence on total numbers. A strong correlation between precipitation and population numbers was observed by Ljundstrom et al.(1973) and Van Rhee et al.(1973). Van Rhee et al.(1973) stated that these changes in population numbers were strongly associated with changes in age class distribution. During wet mild years reproduction increased and a larger number of juveniles were added to the population. This observation is supported by Nordstrom and Rundgren(1974) who noted that moisture was extremely important to the activity and survival of cocoons and juveniles which are exposed to greater variability in soil conditions. This observation may not only apply to juveniles and cocoons but to entire ecological groups which inhabit the soil near the surface. Phillipson et al.(1976) found that population numbers for *Dendrobaena mammalis and L. castaneus* (litter dwellers) were strongly correlated with soil drying, but this did not hold true for mineral soil dwelling species studied.

2.5.2.2 Soil Temperature

Soil temperature affects the metabolism, growth, respiration, and reproduction of earthworms (Minnich,1977;Lutz et al.,1947;Edwards and Lofty, 1972;Barley, 1961).

Although earthworms can not survive prolonged exposure to temperatures at or below freezing similar mechanisms to those used for escaping adverse soil moisture may be utilized to avoid unfavourable temperatures(Lee, 1959;Edwards and Lofty, 1972). Cooler temperatures can reduce fecundity and hatching(Edwards and Lofty, 1972) but do not change species distribution(Nordstrom and Rundgren(1974).

Determining the upper limit in temperature for the survival of earthworms is more difficult since higher temperatures often occur in association with reduced soil moisture. As a result it is difficult to separate out the effects of the two factors(Nordstrom and Rundgren,1974). Edwards and Lofty(1972) stated the upper limit for *L. terrestris* was between 25-29°C. There appears to be no record available for maximum temperatures for other species of earthworms although one would expect them to be highly variable.

Reynolds and Jordan(1975) determined the optimal temperature for six species of earthworms as ranging from 12°C to 25°C. These results were not considered surprising once the ecological niches of the different species were taken into consideration. For example, *Eisenia foetida*, a manure inhabiting species, had an optimal temperature of 25°C, *D. rubida*, a bark dwelling species had an optimal temperature of 18-20°C and the soil dwelling species *Aporrectodea turgida* had an optimal temperature of 12°C.

2.5.2.3 Soil Reaction

Considerable disagreement exists as to the importance of soil pH in determining distribution and population numbers of earthworms. Edwards and Lofty (1972) felt that pH limits the distribution, numbers and species found, while Satchell(1980) claimed that no relationship exists between distribution and pH. Yet Laverack(1961) found nerves in the epidermis of earthworms which are sensitive only to pH. Much of this confusion appears to arise from attempting to generalize about the behavior of earthworms.

The most common statement made is that earthworms prefer a pH near neutral(Edwards and Lofty,1972). A closer examination of the literature shows this is not totally correct. At pH's which approach neutrality total population numbers are highest(Allee et al., 1930;Nordstrom and Rundgren, 1974;Pierce, 1972) but several species have been observed to do well in, or even be preferentially adapted to, pH conditions well away from neutral. The occurrence of different species under widespread pH conditions appears to be related, as with soil moisture and temperature, to the earthworms ecological niche. The distribution of litter or surface feeding species such as *Lumbricus rubellus* and *Dendrobaena* sp., is relatively pH independent(Pierce, 1972). *Dendrobaena* sp. along with *Bistmatos eiseni* and

Eukerrias halophila, two other surface feeders, have even been termed acidophilic(Phillipson et al., 1976;Ljundstrom et al., 1973;Nordstrom and Rundgren, 1974). The species *Arctiostrotus simplicigaster vancouverensis* occurred in soils having a range in pH from 2.6-6.2. The highest population numbers were recorded at sites with a pH of 2.9(Spiers et al., 1983). Pierce(1972) related this association of litter feeding species and acidic soils not to pH directly but to calcium availability. The calciferous glands of earthworms serve the function of controlling the acid-base balance of the body(Laverack, 1963). The litter feeding species have very active calciferous glands which enable them to inhabit acid soils where calcium is concentrated in the litter(Pierce, 1972). Conversely, mineral soil feeders have less active calciferous glands and are more restricted in the range of soil pH's in which they can exist. Indeed species such as *Allolobophora caliginosa*, *A. nocturna*, *A. chlorotica* and *L. terrestris*, which are mineral soil dwellers, are dominantly found in soils with near neutral pH's or are considered acidophobic (Nordstrom and Rundgren, 1974;Phillipson et al., 1976;Pierce, 1972). No record of species inhabiting soils with a highly alkaline reaction exist with the exception of *Helodrilus oculatus* which Pierce(1972) observed to occur exlusively on sites of high pH.

2.6 Overview of Earthworm-Soil Research

2.6.1 Earthworms and the Development of Soil Structure and Humus Forms

Earthworms can change soil morphology in a variety of ways which include disturbance, mixing and aggregation of the soil, formation of channel structures and incorporation of organic matter(Rogaar and Boswinkel, 1978). The study of soil fauna and their role in the development of structural units and humus forms originates largely from morphological observations at the field and microscopic level. It may also be inferred that earthworms are important in the formation of structural units from aggregate stability studies. These will be discussed in a subsequent section on earthworms and soil physical properties in the context of stability of aggregates as opposed to formation of structural units.

Several observations made at the field level indicate the importance of earthworms in the development of surface horizons having a granular structure. Nielson and Hole(1964) found that the earthworms *L. terrestris* and *A. caliginosa* were a dominant force in the development of coprogenous A1 horizons of forest soils in Wisconsin. In Dakota worm-worked soils were considered to be so distinctly different in their morphological, chemical and physical properties that Buntley and Papendick(1960) suggested they be classified as Vermisols. The activity of earthworms resulted in the formation of a strongly expressed secondary structure of subangular to angular aggregates down into the B and C horizons as opposed to the classical long medium prisms of the associated chernozems. Earthworm species such as *L. terrestris, L. festivus, A. tuberculata* and *D. octaedra* were found to dramatically alter the profiles of virgin podzols after invading these soils for a period of only three years(Langmaid, 1964). Typically F, H and Ae horizons and the upper portion of the Bfh horizon were homogenized into a singular horizon having a strong coarse crumb structure.

At the microscopic level the majority of work involving soil fauna has focussed on their role in the genesis of humus forms rather than modifications to structure in subsurface horizons. For this reason the following discussion will emphasize differentiations made between humus forms. Examples of humus forms in which other soil fauna play an important role in development will be included to provide a contrast to humus forms in which earthworms play a unique role.

The concept of terrestrial humus forms was originated by P.E. Muller in 1879. These forms are commonly referred to as mull, mull-like mor(moder) and mor(Barratt, 1964). Kubiena(1955) emphasized that the humus form is not a chemical concept referring to a group of organic substances, but comprises the organic and inorganic components of soil and the way in which they are mixed or combined. In addition the humus form connotates the formation of a typical humus profile and is associated with a typical complex of soil biota and their activities.

Barratt(1964) stated that Kubiena(1953) described numerous microfabrics but did not relate these to the horizons of the humus forms in which they occurred. She attempted to show these relationships by describing the microfabrics of twelve humus forms occurring in soils of temperate grasslands. Although the fabric descriptions were based on grassland humus forms Barratt(1964) emphasized that they are very similar to their forest counterparts but are less well defined, possibly because of the difference in diversity and quality of plant species involved. The humus forms described ranged from weak and strong mull humus to mull-like moder, moder and raw humus. Earthworm casts were considered to dominate the fabric of the strong mull humus and enchytraeid droppings dominated the mull-like moder fabric. The activity of insects such as mites and collembola dominated the formation of most moder humus forms while fungal activity was considered to be the dominant agent active in the formation of raw humus forms. Babel(1975) described six different humus forms after examining profiles from a variety of ecosystems including forests, natural grasslands and pioneer vegetation. The humus forms he described were mostly mull and moder types. Only earthworms were implicated in the genesis of mull humus forms while enchytraeids dominated the formation of mull-moder and moder forms. Thus, the work of these individuals appears to support the claim of Kuhnelt(1958) that earthworms and enchytraeids are the only animals which build up clay-humus complexes(i.e. mull humus forms) in soils of temperate regions while others build moder. Although this statement may be true it should not be interpreted as meaning these fauna are exclusively involved in the formation of mull humus forms, only that they are agents capable of promoting the process of mull formation.

Reflecting back on the ecological classification system for earthworm species one group was defined by Perel(1977) as soil surface or litter dwellers which consumed only slightly decomposed plant residues(Type I - Group 3). Species such as *D. mammalis, E. foetida and L. castaneus,* which belong to this group, function almost exclusively in the litter layers. It is logical to assume these species are involved in the formation of moder and mor as opposed to mull humus forms as their contact with the mineral soil is minimal, at best only occurring during periods of relative inactivity while avoiding adverse moisture and temperature conditions in the litter layer. Indeed this appears to be true. Bal(1970) when studying the genesis of moder-humus profiles determined that *D. rubida* played a dominant role in the formation of an H1 humus layer under red oak. This earthworm acted as a secondary devourer of orbatid mite excrement, thus contributing to the aging process of the humus profile in a zone well above the mineral soil. Similarly Dinc et al.(1976) consistantly referred to the role earthworms played in the aging process and development of peat soils and Barratt(1964) referred to "small red worm droppings" as contributing to a mull-like moder redzina. Recently, on Vancouver Island, the classification of a mor humus form resulting from the activities of *Arctiostrotus simplicigaster vancouverensis* even became problematic since the taxonomic system utilized in the area for humus forms did not accomodate for mor or moder forms resulting from earthworm activity(Spiers et al., 1983).

2.6.2 Earthworms and Soil Physical Properties

Earthworms frequently have been observed to affect a wide variety of soil physical properties. These effects are largely the result of earthworms influencing structural development, creating channeling systems and integrating organic matter into the surface horizon. Wollny (in Teotia et al.,1950) was the first to record the positive effects of earthworms on soil physical properties. He concluded they increased infiltration rates and non-capillary porosity. Since that time numerous studies conducted on earthworms and their influence on soil physical properties have all lead to positive conclusions.

A two to five fold increase in aggregate stability of earthworm worked soils over corresponding controls has been observed consistantly(Teotia et al., 1950; Hopp and Hopkins, 1946;Pierce, 1981;Van Rhee, 1977). Teotia et al.(1950) found the stability of aggregates to vary with the texture of soil and species of earthworm involved. Aggregate stability was found to be highest with *Helodrilus caliginosa* and lowest with *Diplocardia riparia*. The stability of earthworm formed aggregates in fine sand approximated that of the original soil, those in loams were twice as stable as the original soil while aggregates formed in clay soils were the most stable. Aggregate stability also increased if organic matter additions accompanied the earthworms and varied with the nature of the addition(Teotia et al., 1950;Swaby, 1950).

The reason why aggregates formed by earthworms are more stable to destruction by water is poorly understood. The most popular notion is that aggregates(or castings) are stabilized by microbial gums synthesized by the increased number of micro-organisms commonly recorded in faecal material(Swaby, 1950). Hopp and Hopkins(1946) contested this notion when they found incubating castings did not increase their stability. The authors concluded the aggregates must already be stable when expelled from the earthworms gut and not through a subsequent increase in microbial activity. Dawson(1947) supported this conclusion after comparing the stability of control soil material, casts and aggregates extracted from the earthworms gut. He found that lowest bacterial numbers occurred in association with the most stable aggregates originating in the earthworms gut and suggested these aggregates were bound by metabolic products excreted in the gut. Pierce(1981) felt that frequently, in culture studies, aggregation was observed to occur so rapidly that it could not be due to casting. He collected the mucus secreted through the exterior of the earthworms body from various species and tested its ability to bind sand. The results in order of increasing ability to bind sand were as follows:

control<*A. longa*,*L. terrestris*<*L. rubellus*<*E. foetida*

Pierce(1981) also ran pot experiments where starved *L. terrestris* (i.e. no casting contributed to the soil) significantly increased the aggregate stability of the soil in which they existed.

Other soil physical properties such as water retention, aeration, infiltration and drainage are influenced by changes in porosity and pore size distribution brought about by earthworm activity. This, in turn, is determined by the burrowing and feeding habit of the earthworm so one may expect the nature of the effect to vary according to the species of earthworm.

In general earthworm activity leads to an increase in water retaining capacity and aeration porosity. Guild(1955) ran pot experiments where control and worm-worked soils were kept at similar moisture contents. The control soil was soggy, structureless and water was held in the saturated state to the total exclusion of air. In the worm worked soil moisture was held within the aggregates and surplus water drained out permiting an increase in aeration porosity. Similar observations were made in the field(Van de

Westeringh, 1972). Inoculating a newly drained polder with *A. caliginosa* increased total porosity and the percent of large capillary pores where water was less tightly bound(Van Rhee, 1969b). The percent water between pF 4.2(wilting point) and pF 2.2(field capacity) was 37.3% where earthworms were present as opposed to 26.5% where they were absent. On these same plots the increase in porosity was found to correspond with a three fold increase in air permeability(Rogaar and Boswinkel, 1978). The influence earthworms have on water retention was shown to vary with species(Guild, 1955). Mineral soil dwellers such as*A.longa*, *A.caliginosa* and *L.terrestris*, increased water retention significantly, while litter dwellers such as*L. rubellus* and *D.subrubicunda* did not.

Increases in pore volume have been attributed to channels built by earthworms while tunnelling and in the surface horizons due to pores in and between surficially deposited casts(Ehler,1975;McColl et al.,1982;Rogaar and Boswinkel, 1978;Van de Westeringh, 1972;Van Rhee,1969b). This increase is often associated with an increase in the percent of non-capillary pores which are important to the drainage of free water(Van de Westeringh, 1972; Ehlers, 1975). Earthworms are generally thought to increase infiltration rates and improve drainage(Slater and Hopp, 1947;Carter et al., 1981;Ehler, 1975). In this respect it is important to recognize that strong differences exist between the tunnelling behavior of ecological groups of earthworms.

The configuration of the tunnelling systems will, in turn, determine the magnitude of their impact on drainage and infiltration(Kirkham, 1982). Rogaar and Boswinkel(1975) described two distinct burrow morphologies. The first type, attributed to the activity of *Allolobophora* sp., occurred dominantly in the upper 18 cm, had a twisted morphology where burrows ranged from 0.8-5.0 mm. in diameter and were commonly infilled with faecal material. The second type, resulting from the action of *L.terrestris*, had diameters up to 8.0 mm. and predominantly vertical orientations down to a depth of 96 cm. Obviously the permanent channels constructed by *L.terrestris* which are open to the surface would be much more effective in increasing infiltration rates and improving drainage as opposed to those constructed by *Allolobophora* sp. which were non-permanent and discontinuous, occuring only at the soil surface. This is supported in a study by Abbott and Parker(1981). *E.foetida*(a species active at the surface) did not improve drainage significantly while *Microscolex dubius*(a surface feeding mineral dwelling species) increased infiltration significantly through the tunnels created when coming up to the surface to feed.

2.6.3 Earthworms and Decomposition

It is commonly accepted that earthworms are instrumental in accelerating the process of decomposition. The nature and magnitude of their influence varies depending on the species of earthworm involved, the quality and quantitity of organic matter additions and the nature of the decomposer community inherent to the site.

At the field site level the idea that earthworms accelerate decomposition has been inferred after observing the removal of litter in the presence of earthworms, or the accumulation of litter where earthworms have been eliminated. After the invasion of virgin podzols by earthworms LFH horizons ranging from 2.5-5.0 cm in thickness were completely mixed into the mineral soil(Langmaid, 1964). The decomposition of straw was increased from 10-50% depending on the number of earthworms present (Atlavinyte and Pociene, 1973a). The accumulation of undecomposed plant material commonly occurred where agronomic practices had resulted in a decrease or elimination of earthworm populations (Van de Westeringh, 1972;Cook et al., 1975;Rogaar and Boswinkel, 1978). Stout and Goh(1980) evaluated d^{13} C(bomb radiocarbon) in order to demonstrate the effectiveness of earthworms at incorporating organic matter into the mineral soil. In two hardwood stands where earthworms were absent plant litter was enriched in bomb radiocarbon at 5-0 cm while at 0-10 cm older carbon was detected in low quantities. This indicated no significant incorporation of recently deposited litter had occurred. Conversely, where earthworms were present, no litter had accumulated and the top 10 cm was higher in both total carbon and radiocarbon. A similar effect was demonstrated by the same authors in grassland ecosystems.

Although Satchell(1967) claimed that it is difficult to estimate the quantity of plant and other organic materials eaten or buried by earthworms some estimates are available. Populations of *L. terrestris* were observed to completely remove annual litter fall in a period of less than one year(Hazelhoff,1981;Cook et al.,1975). Similarly Nielson and Hole(1964) found 46 leaves/year were gathered into middens of *L. terrestris*. Taking into consideration the number of middens per acre they calculated the amount of litter translocated by these earthworms closely approximated estimates for average annual leaf fall in the same forest. Only two years after their introduction into vegetatively reclaimed coal mine spoils *L. terrestris* buried or consumed 81% of the litter and 43% of the humus which would have otherwise accumulated (Vimmerstedt and Finney, 1973). These estimates indicate that significant amounts of litter are removed from the surface and integrated into the soil but they are based on the action of a single species of earthworm, namely *L. terrestris*, which is a deep burrowing surface feeding species. Again it must be emphasized that conclusions drawn regarding the activity and influence of this species should not be applied to all earthworms. *A. caliginosa*, a mineral soil dweller, feeding on decaying plant matter(Type II-Group II;Perel, 1977) had no effect on straw decomposition after six months, but after ten months a noticeable effect was evident(Atlavinyte, 1971). This indicated that some predisposition of the straw was necessary before the accelerating affect on the decomposition process was brought about by the activity of this species. In the study by Stout and Goh(1980) surface dwelling species were present in the forest litter layer which was enriched in bomb radiocarbon and had accumulated at the soil surface. Even though earthworms were present their impact on reducing the accumulation of litter was apparently minimal. These examples serve to re-affirm that the magnitude and nature of the effect earthworms have on soil processes largely depends on their ecological niche.

In terms of ecosystem dynamics it is of greater importance to evaluate the chemical and physical alterations to organic matter additions under the influence of earthworms and not only the total amounts of litter "buried or eaten". There remains little doubt that earthworms alter the physical constitution of ingested organic matter, comminuting litter and increasing its exposure to microbial and enzymatic attack (Nielson,1962;Bolton and Phillipson,1976;Heungens,1969;Arthur, 1965). The question of how or if earthworms chemically alter ingested organic matter, and to what extent, is much more controversial and less well understood.

In order to examine this question critically two aspects must be considered.

1. Partitioning of ingested organic matter into the fractions assimilated, transformed and/or egested and,
2. Through what mechanisms and where are chemical transformations occurring.

The feeding preferences and behavioural patterns of different groups of earthworms will determine the relative proportions of organic versus inorganic material ingested, as well as the quality of organic matter ingested. The end products of ingestion and their relative proportions vary accordingly. Piearce(1978) studied the gut contents, particularly that of the crop and gizzard, in six species of lumbricids including *A. caliginosa*, *A. chlorotica*, *A. longa*, *D. mammalis*, *L. castaneus*, and *L. rubellus*. *L. castaneus* and *L. rubellus* took in the highest amounts of organic fragments. These were in a relatively undecomposed state. *A. caliginosa* and *A. chlorotica* ingested the least amount of organic matter most of which consisted of well decomposed detritus. Ingestion of organic matter by *A. longa* and *D. mammalis* was intermediate between the above two groups where no preference for organic matter in a particular state of decomposition was shown.

Differences also exist between species in regard to the transit time of gut contents(Table 2) and ability to assimilate organic constituents. This in turn determines the proportions of organic matter assimilated, transformed and/or expelled.

Table 2:Gut transit times for different species of earthworms

Species	Transit Time	Reference
L. rubellus and A. caliginosa	13-24 hours	Piearce, 1972 Barley, 1959
L. terrestris	20 hours	Parle, 1963 Satchell, 1967
E. foetida	2.5 hours	Hartenstein et al., 1981
A. rosea	1.9 hours	Bolton et al., 1976

Hartenstein et al.(1981) found the gut transit time for *E. foetida* was 2.5 hours. It was independent of whether mineral or organic matter was ingested as well as the weight or length of the earthworm. Conversely, transit times could range from .85 hours for small earthworms to 2.19 for large earthworms of the species *A. rosea*(Bolton and Phillipson, 1976). Kretzschar(1977), when studying populations of *Nicodrilus longus* and *N. nocturnus*(Evans) var. *cistereianus*, found no differences in gut transit duration during the same season, between stages, taxa or weight and length classes of earthworms. He did find that durations were quickest in the spring, followed by the fall and lastly the winter, probably reflecting the availability of food and soil temperature.

Crossley et al.(1971) used ^{134}Cs labelled forest litter to study the passage of organic matter through the gut of *O. lacteum*, *E. hortensis* and *L. terrestris*. Using this method they were able to determine the proportions and turnover rates of organic matter assimilated and egested by the various earthworms. They referred to the non-assimilated portion as the "short component" and the assimilated portion as the "long component" because of the large difference in their turnover rates. For example, with *O. lacteum*, T1/2 for the short component was 5.8 hours and T1/2 for the long component was 6.2 days. *O. lacteum*(top soil dweller) assimilated the lowest proportion of organic matter ingested and once excreted this component had the longest turnover rate. *E. foetida*(litter dweller) had similar turnover rates to that of *O. lacteum* for the gut contents, but assimilated a higher proportion of the organic and this component turned over at a faster rate. *L. terrestris*, on the other hand, assimilated a similar proportion of ingested litter to that of *E. foetida* but the turnover rate of this material was highest relative to both the other species. The turnover rate of the gut contents of *L. terrestris* was the lowest of all three species studied. Little further information is available regarding the amount of ingested organic matter which is assimilated by earthworms. Proportions of 11.6%, 28.5% and 25.4% were considered to be digestively assimilated by *O. lacteum*, *E. foetida* and *L. terrestris*, respectively(Crossley et al., 1971). Comparative figures of 1.4%, 2.0% and 2.4% were determined for adults, large immatures and small immatures of the species *A. rosea*(Bolton and Phillipson, 1976). Because of the limited amount of information regarding assimilation rates and how they differ between species according to their ecological niche and behavioral patterns it is difficult to make any definitive statement regarding the impact of earthworms on the dynamics of organic matter turnover. Indications are that litter dwelling species(including immatures belonging to other ecological groups) ingest the largest proportions of relatively undecomposed organic matter. Assimilation rates for this group fall into an intermediate range but gut transit times are shortest. The net effect of this group of earthworms on organic matter transformations and turnover rates may be the greatest. Topsoil dwelling species appear to play the least important role in organic matter turnover since they ingest the lowest proportion of organic matter which is already in a relatively decomposed state. The proportion of organic matter assimilated and the turnover rate of the long component was the lowest for *O. lacteum* in the study by Crossley et al.(1971). Lastly, deep burrowing litter feeding species, such as *L. terrestris*, may play a role secondary in importance to the litter dwelling species in terms of organic matter dynamics. *L. terrestris* ingests relatively high proportions of undecomposed organic matter. It was shown to have assimilation rates similar to *E. foetida*, the highest turnover rate of the short component but much longer gut transit times(Crossley et al.,1971;Table 2).

There is further debate as to whether chemical transformations of ingested organic matter occur directly in the earthworms gut, either through the action of digestive enzymes or gut flora, or if the acceleration of the decomposition process by earthworms is an indirect effect on the decomposer community where microbial processes are influenced after the egestion of faecal material.

The controversy over the enzymatic capability of earthworms has, for the most part, been discussed in the context of nutritional requirements of earthworms(section 2.5.1). Nielson(1962) stated that it is ecologically unimportant to know whether enzymes found within the earthworm are produced by gut flora or the animals themselves as long as their existance and functional importance can be determined. Many questions in this regard still remain unanswered. Frequently cellulase activity has been detected in the gut of earthworms and the conclusion drawn that these fauna must be instrumental in the decomposition process(Mishra and Dash, 1980;Table 1). Nielson(1962) pointed out that detection of cellulase activity alone does not automatically imply that earthworms can degrade plant material. Structurally and chemically plant materials are very complex and numerous other enzymes must accompany the action of cellulase in order to complete its breakdown. As yet, many of these other enzymes have not been detected in the gut of the earthworm. In addition, cellulase assays are often carried out using hydrolyzed or soluble forms of cellulose. In nature, and particularly in reference to earthworms, little is known regarding this initial step of converting native cellulose to a soluble form(Nielson, 1962). Even though numerous kinds of enzyme activities have been detected in the earthworms gut it remains unknown if they are utilized in the breakdown of plant material. Arthur(1965) felt that, if anything, hydrolysis of cellulose was effected by gut enzymes, since the length of time food remains in the gut is not long enough for microbial enzymes to have any significant influence. A statement of this kind presupposes a firm knowledge of both gut transit times and enzyme kinetics within the environment of the gut of the earthworm. This type of information is lacking for a single species of earthworm and considering the known variability in gut transit times that exists between species, it becomes unreasonable to accept the generalization made by Arthur(1965). Few enzymes have been universally detected in all species of earthworms for which assays have been performed(Mishra and Dash,1980;Khambata and Bhat, 1957) possibly indicating that depending on the species, different enzyme complexes have evolved as an adaptation to their ecological niche and food supply.

Although the issue of enzymatic capability and the origin of the activity remains controversial the notion that earthworms have a marked influence on microbial activities in the soil is more commonly accepted. Atlavinyte et al.(1977) concluded that the direct effect of earthworms on plant decomposition was much less pronounced than their indirect affect through influencing the size of the decomposer community.

Increases in microbial numbers in the order of two to five times in faecal material and/or soil in which earthworms were active have commonly been recorded(Atlavinyte et al., 1969;Atlavinyte et al.,1977;Atlavinyte et al., 1980;Kozlovskaja, 1969;Loquet et al., 1977;Czerwinski et al., 1974;Ausmus, 1977). The magnitude of the increase may depend on the size of the microbial population inherent to the soil. Czerwinski et al.(1974) found that no significant increase occurred in earthworm casts when microbial numbers in the control were already high but significant increases were recorded where numbers were inherently low. Further evidence indicates that earthworms do not necessarily inoculate the soil with new microbial organisms and thus accelerate the decomposition process, but rather they alter the qualitative and quantitative balance of the existing decomposer community. Through this action they can enhance the intensity and direction of microbial processes already occurring. The direction microbial processes take under the influence of earthworms is a function of soil type, microflora and the quality and quantity of organic matter ingested (Kozlovskaja, 1969;Czerwinski et al., 1974;Petal et al.,1977).

Although scanty, evidence exists to support the concept of Ausmus(1977) in regards to the role that channelizing invertebrates play in the decomposition of wood. This concept may be more broadly applied to decomposition in other ecosystems. Ausmus(1976) described channelizing invertebrates as essential rate regulators of wood decomposition, altering the substrate as a result of comminution, affecting the available inoculum, removing readily available materials and shifting the competitive advantage from fungal to bacterial populations. The cumulative effect of these activities allows for an increase in nitrogen fixation and carbon catabolism. Four mechanisms for the regulation of wood decomposition by invertebrates as postulated by Ausmus(1976) are as follows;

1. translocation and defecation increase nutrient input to, and the inoculum potential of, wood substrates;
2. passive inoculation, as in the case of wood-surface colonizing invertebrates passively inoculating wood and predisposing wood substrates to fungal and subsequent channelizing invertebrate colonization;
3. microbial succession and the rates of microbial catabolism are regulated by invertebrate dynamics, creating successive waves of temporally distinct periods of time when nitrogen is atmospherically fixed and carbon rapidly catabolized; these successional waves stabilize and increase microbial respiration and probably microbial catabolism rates;and

4. by creating spatial heterogeniety within woody substrates and microsites of intense physical-chemical-biological activity.

Several observations regarding earthworms and their interaction with decomposer organisms tends to support this hypothesis of Ausmus(1976). Low carbon utilization of organic matter passing through the gut indicates that the earthworm most likely assimilates the readily available sources of organic carbon and egests the resistant fraction(Bolton and Phillipson, 1976). Earthworms are highly proteinaceous(French et al.,1957) and may be expected to preferentially assimilate nitrogen. Syers et al.(1979) found that 73% of the total nitrogen in removed litter was accumulated in surface casts, implying 27% must be utilized by the earthworms. They considered this a relatively poor efficiency of nitrogen utilization, however it can be considered relatively high compared to the 2.5% carbon utilization estimated by Bolton and Phillipson(1976). The net effect of preferential assimilation of nitrogen, low carbon utilization and removal of the more labile organic fraction during passage through the gut results in the excretion of higher C:N material in the casts. In fact, C:N ratios of faecal material have been observed to be higher than that of control soil material(Table 3).

Earthworms also appear to cause a qualitative shift in microbial populations in a manner such as that proposed by

Table 3:C:N ratios of casts and associated control soil material

Casts	Control Soil	Reference
10.7	15.0	Syers et al.,1979
14.7	13.8	Lunt et al.,1944
25.1	18.0	Lunt et al.,1944
10.7	7.9	Watanabe,1975
8.5	15.9	De Veeschauwer et al.,1981
8.2	7.2	De Veeschauwer et al.,1981
8.7	5.7	De Veeschauwer et al.,1981
8.3	4.5	De Veeschauwer et al.,1981
9.7	7.0	De Veeschauwer et al.,1981
12.1	6.4	De Veeschauwer et al.,1981

Ausmus(1976). Earthworms have been observed to preferentially ingest or cause a decrease in the number of fungi which would aid in causing a temporal shift from fungal to bacterial populations as described by Ausmus(1976)(Cooke et al.,1980;Kozlovskaja,1969). Further, spore forming bacteria(*Bacillus* sp.) have been observed to survive passage through the gut of earthworms(Edwards et al.,1977;Day,1950;Kozlovskaja,1969) and numbers of cellulolytic and nitrophilous microorganisms have been shown to increase in freshly deposited casts(Loquet et al.,1977;Kozlovskaja,1969;Czerwinski et al.,1974;Petal et al.,1977). Thus, the shift in microbial populations temporarily gives the competitive edge to those organisms capable of attacking more resistant materials and accelerating the process of decomposition.

Some evidence for enhancement of nitrogen fixation in soils under the influence of earthworms, lends further support to the hypothesis of Ausmus(1976). Khambata and

Bhat(1957) cultured 31 isolates on nitrogen free media from the gut of earthworms. They emphasized the isolates were not assayed for the capability to fix atmospheric nitrogen. Bhat(1974) stated that earthworms are instrumental in "Azotobacterization" of soil, disseminating *Azotobacter* which he had shown were associated with the alimentary canal and castings of earthworms. Both Loquet et al.(1977) and Ausmus(1976) showed that significant rates of acetylene reduction were associated with faecal tunnel linings of different species of earthworms indicating that atmospheric nitrogen fixation may indeed be enhanced by these soil fauna. Ausmus(1976) emphasized that ^{15}N experiments are necessary to confirm that atmospheric nitrogen fixation was indeed occurring in association with earthworm activity.

Although fragmentary this evidence indicates that earthworms may function in the decomposition process in the manner postulated by Ausmus(1976). Obviously it is necessary to undertake more studies in order to confirm the hypothesis. Most likely, as with other soil processes affected by earthworms, numerous factors such as the species of earthworm, its feeding habits, the quality and quantity of organic matter ingested and the ecosystem under consideration will strongly affect the direction and nature of microbial processes as influenced by earthworms.

2.6.4 Earthworms and Nutrient Cycling

Research into the subject of earthworms and their involvement in basic nutrient cycling is far more limited in scope than investigations into their role in decomposition even though both processes are intimately associated(Krivolutsky et al.,1977). It has been determined frequently that the availability of nutrients increased in soils where earthworms were active(Teotia et al.,1950;Lutz et al.,1947;Lunt and Jacobson,1944;De Vleeschauwer et al.,1981). This has commonly been attributed to earthworms preferentially ingesting nutrient rich litter and releasing elements by accelerating the process of decomposition(Kale et al.,1980;Krivolutsky et al.,1977). Only a dearth of information is available regarding earthworms and their involvement in the cycling of elements such as Mg, Na and K. The emphasis has been placed on the cycling of Ca, mainly because of the presence of calciferous glands in a large number of species of earthworms. Most genera of British origin possess both glands and pouches, but the latter are lacking in genera such as Eisenia and Helodrilus(Arthur,1965).

The majority of literature available indicates that earthworms utilize the formation of $CaCO_3$ in order to maintain the acid-base balance of their body. The calciferous glands are the most important organ in the earthworm which influence this equilibrium. The net effect on the soil system is reflected in changes to soil pH, and the form(soluble vs. insoluble) in which Ca exists. The $CaCO_3$/carbonic acid/bicarbonate equilibrium within the earthworms body is dependent on the following factors:

1. Presence or absence of calciferous glands and/or pouches in the earthworm.
2. The level of activity of the calciferous glands.
3. The level of CO_2 concentrations in the earthworms external environment or in the earthworms body as a result of metabolic activity.
4. The availability of soluble and diffusable Ca.
5. The presence or absence of $CaCO_3$ in the soil.
6. The chemical nature of material ingested by the earthworm.

It is important to understand the function of the calciferous glands and the mechanisms through which they act in order to fully appreciate the role earthworms play in the cycling of Ca. Arthur(1965) and Laverack(1963) provided ample evidence to indicate that the primary function of the calciferous glands is to control the CO_2 concentration, and therefore the acid-base balance, of the earthworms body fluids. Laverack(1963) described two mechanisms whereby $CaCO_3$ is synthesized in the calciferous gland region(Fig. 1). The first involves the action of carbonic anhydrase to form carbonic acid which under the prevailing conditions of pH dissociates to form bicarbonate. The bicarbonate reacts with Ca^{++} which is concentrated in the lumen of the glands through a process of filtration. This mechanism probably

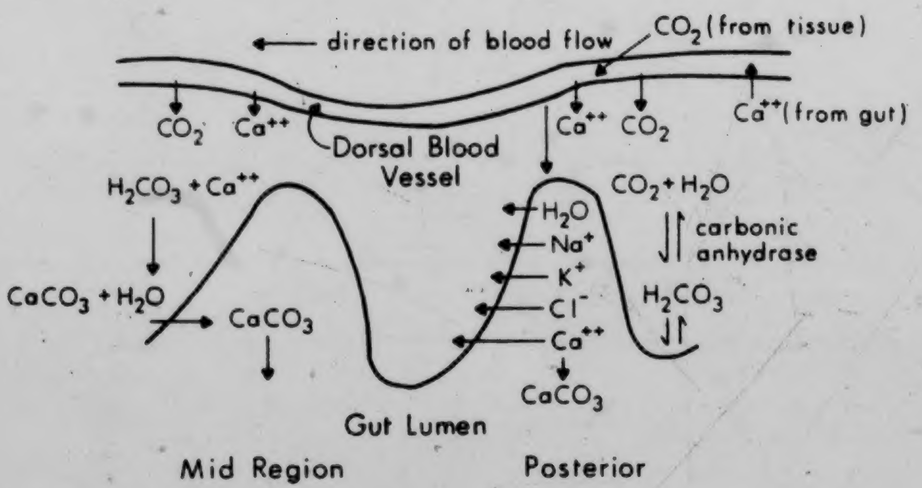

direction of blood flow
CO_2 (from tissue)
CO_2
Ca^{++}
Dorsal Blood Vessel
Ca^{++}
CO_2
Ca^{++} (from gut)
$H_2CO_3 + Ca^{++}$
$CaCO_3 + H_2O$
$CaCO_3$
H_2O
Na^+
K^+
Cl^-
Ca^{++}
$CaCO_3$
$CO_2 + H_2O$
carbonic anhydrase
H_2CO_3
Gut Lumen
Mid Region
Posterior

Figure 1:Formation and secretion of $CaCO_3$ concretions from two areas in the calciferous glands. (after Laverack,1963)

dominates due to the rapidity of the catalyzed formation of carbonic acid and the fact it occurs in the posterior region of the glands. The second mode of formation occurs in the mid region of the glands. Once the blood has reached this region its constitution has been modified so that $CaCO_3$ is formed within the glands and is released by rupture of the cells into the lumen.

In natural systems the formation of $CaCO_3$ by earthworms can result in significant alterations to the reaction, and therefore the chemical environment, of the soil system. Wiecek et al.(1972) concluded that spheroids of $CaCO_3$ found in the A1 horizon of otherwise acidic forest soils were biologically synthesized through the action of earthworms. The pH of the A1 was 8.0 where 2.55 gm. spheroids/m^2/25cm and was 6.2-7.8 where .83 gm. spheroids/m^2/25cm were found. pH values in excess of 7.0 were attributed to the weathering of the calcite spheroids.

In the early literature it was proposed that $CaCO_3$ formed in the calciferous glands was used to neutralize acidity in the gut arising from decomposition of ingested organic matter(Laverack.1963). Robertson(1939) and Arthur(1965) rejected this idea but evidence presented by Kale et al.(1980) indicated the hypothesis may be valid. They studied the partitioning of Ca in earthworms and soil after the earthworms were active in calcareous material. Ca in the ionic, exchangeable and/or soluble form was determined in the calciferous gland region, body and gut of the earthworm as well as in the soil material before and after passing through the earthworm. Only a slight increase in total Ca in the castings was determined but large differences in the form in which the Ca occurred were found(Table 4).

Table 4:*Pontoscolex corethrurus*:Calcium and carbonates in soil and castings.(after Kale et al.,1980)

	ug/g dry weight	
Constituent	Soil	Castings
Ionic Calcium	12.24±.41	145.00±9.81
Exchangeable Calcium	12.83±.37	95.23±7.28
Insoluble Calcium	179.62±.02	32.09±0.93
Ionic/Insoluble Calcium	0.15±.01	6.98±2.22

The majority of Ca in the castings was excreted in an ionic form as opposed to the original soil material where the largest percent of Ca occurred in an insoluble form. It was determined that the pH values within the earthworm increased from 6.8 in the gizzard region to 8.4-9.3 in the intestine. These observations led Kale et al.(1980) to conclude that secretions from the calciferous glands were important in raising the pH within the earthworms intestine. It was inappropriate for the authors to conclude that it was the $CaCO_3$ secreted by the calciferous glands which dissociated in the gut to control pH, and not $CaCO_3$ ingested by the earthworm from the soil. None the less, they presented evidence which indicates that dissociation of $CaCO_3$ occurs in the gut to buffer pH, regardless of the source. Laverack(1963) suggested that in addition to controlling body fluid acid-base balance equilibrium the calciferous gland of earthworms living in calcareous habitats may be used to maintain their salt and water balance. Such species are known to have larger glands than those inhabiting less calcareous soils.

The available evidence suggests that $CaCO_3$ from the soil and secreted by the calciferous glands are both sources of material for buffering the pH of the gut. Stephenson(1930) supported this view by stating that in addition to controlling CO_2 levels the calciferous glands probably have a further use in neutralizing the contents of the alimentary tract. He pointed out the similarity of digestion in the earthworm to pancreatic digestion in higher animals which takes place only in an alkaline medium and provided evidence for increased activity of the glands when earthworms were feeding on acidic organic matter.

The degree in development of the calciferous glands and their activity vary according to the species of earthworm. This, in turn, is important in determining the ecological niche of the earthworm and therefore how it affects the dynamics of Ca cycling. Moursi et al.(1975) found *A. caliginosa*, which possesses active calciferous glands, was able to withstand high doses of CO_2 and function at depths in the soil where CO_2 concentrations are considerably higher than atmospheric. Conversely *Pheretima californica*, which lacks calciferous glands, could not tolerate high doses of CO_2 and therefore holds an ecological niche at the soil surface. Stephenson(1930) pointed out that the presence of calciferous glands is associated with dry environments and a large size of body. The excretion of CO_2 mainly takes place through the body surface where there is a film of water which is continually changing. An alternate mechanism of excretion is needed if the latter condition can not be met. With large species of earthworms the body surface area does not increase sufficiently along with body volume in order to accomodate the increase in respiration, and again an alternate means of excretion is necessary. High activity of the calciferous glands is associated with acid tolerant species such as *Dendrobaena rubida* whose retention of Ca and turnover of litter was determined to be higher than that of acid intolerant species(Ireland, 1975;Pierce, 1972). *Allolobophora sp.* possesses reduced calciferous glands resulting in low retention and turnover of Ca, while *L. terrestris* exhibited high Ca turnover during periods of activity(Anderson,1979). In addition, the stage of maturity of the earthworm can determine the magnitude of its influence on Ca cycling. Kale et al.(1980) found that as the earthworm increased in size less Ca went into the biomass and the Ca binding capacity of the proteins decreased resulting in more Ca being excreted in an ionic form.

A model is presented in Fig. 2 to summerize the mechanisms for acid-base control in the earthworm utilizing $CaCO_3$ equilibrium. The pathways used in any one case will depend on the species of earthworm involved because of its physiology and ecological requirements, the nature of the soil material(calcareous vs. non-calcareous) and the nature of the organic matter ingested by the earthworm.

The available evidence indicates that under acidic conditions species active in the surface layers of the soil dominate. These species are typically small in size but very active. Their demand for Ca is high and the Ca is obtained mainly from organic sources. Cromack et al.(1977) suggested that degradation of organic salts such as Ca-oxalate in the gut of earthworms may also contribute to moderating pH by converting a stronger acid to a weaker one. Large amounts of Ca are retained within the body of these earthworms in order to serve the dual function of controlling CO_2 levels in the body fluids and pH balance in the gut. In calcareous systems one would find larger species of earthworms which burrow deeply and possess well developed calciferous glands. The physiology of these species allows them to function under conditions of high CO_2 and salt concentrations but their retention of Ca is low. The net effect on the soil system is an increase in the available forms of Ca which can be taken up by plants or become involved in other soil reactions.

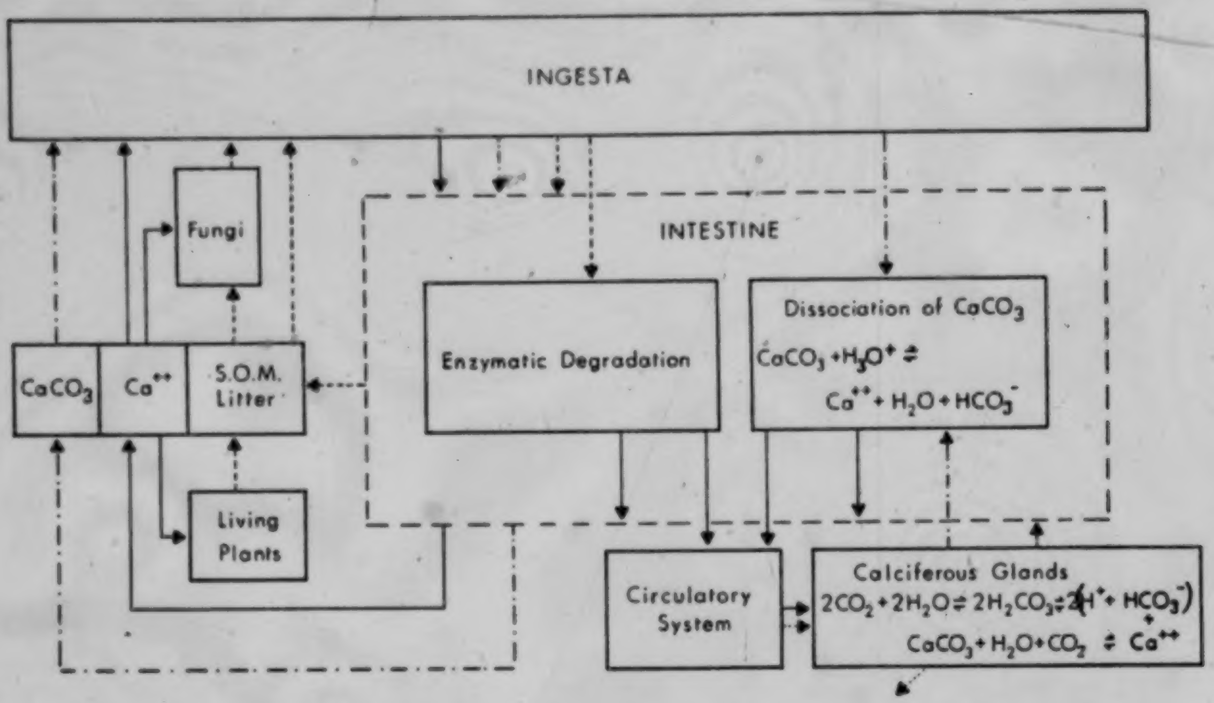

INGESTA
INTESTINE
Fungi
CaCO$_3$
Ca^{++}
S.O.M. Litter
Living Plants
Enzymatic Degradation
Dissociation of CaCO$_3$
$CaCO_3 + H_3O^+ \rightleftharpoons Ca^{++} + H_2O + HCO_3^-$
Circulatory System
Calciferous Glands
$2CO_2 + 2H_2O \rightleftharpoons 2H_2CO_3 \rightleftharpoons 2(H^+ + HCO_3^-)$
$CaCO_3 + H_2O + CO_2 \rightleftharpoons Ca^{++}$

Figure 2:A model for the cycling of calcium and carbonates as controlled by earthworms for the maintainance of body pH.

KEY

——— Ca^{++}
– – – – Ca-organically bound
—·—·— CaCO$_3$
·········· CO$_2$

2.6.5 Earthworms and Soil Management

Numerous studies exist in the literature regarding earthworms and their influence on crop productivity. These studies are primarily concerned with the nutrient uptake and dry matter production of cereal crops. Recent studies in agronomy emphasize cropping and cultivation practices and their influence on the population dynamics of earthworms; the ultimate goal being to promote or maintain a favourable population of earthworms. Earthworms have also been used successfully as an inoculant for reclaiming mine spoils and increasing productivity of drained land and forest soils(Vimmerstedt et al.,1973;Van Rhee,1977;Huhta, 1979).

In agricultural practices increases in dry matter production resulting from the activities of earthworms ranged from 20-200%(Atlavinyte et al.,1968;Atlavinyte et al.,1973b;Atlavinyte et al.,1982;Russell, 1910;Martin et al.,1976;Graff et al.,1980;Abbott et al.,1981). This was attributed mainly to the increase in availability of plant nutrients and improvement in soil physical properties by earthworms. The magnitude of the influence earthworms have on plant nutrient uptake and dry matter production depends on the type of agronomic practices utilized and the nature of the soil. In pot experiments with non-fertilized soils, earthworms increased dry matter production of barley but decreased the amount of ash in the grain(Atlavinyte et al.,1982). When mineral fertilizers were added the influence of earthworms on plant productivity was negligable but when the soil was ammended with straw significant increases in productivity and uptake of nutrients occurred(Atlavinyte et al.,1982;Atlavinyte et al.,1973b).

In order to realize the benefit of increased nutrient availability from the activity of earthworms it is essential that organic matter be returned to the soil. When both earthworms and straw were added to soil, as opposed to straw alone, significant benefits to plants were realized(Atlavinyte et al.,1973b;Atlavinyte et al, 1968;Mansell et al.,1981). The return of organic matter to the soil provides an energy source for maintainance of a beneficial population of earthworms and they, in turn, enhance mineralization processes which return nutrients to the plants in available forms. This is particularly important in influencing the availability of P and N to plants. Where soils were ammended with both straw and earthworms increases in P uptake by plants ranged from 36-68% over controls where only straw was added(Atlavinyte et al.,1973b). Similarly, Mansell et al.(1981) found 2-3 times more P was taken up by plants from ^{32}P labelled casts as opposed to labelled dead herbage.

Indications are that earthworms have an important influence on nitrogen dynamics and therefore the availability of N to plants. While Russell(1910) and Atlavinyte et al.(1982) found live worms had no effect on plant uptake of N, Southwell et al.(1982) and McColl et al.(1982) found earthworm activities resulted in increased N uptake. Earthworms were found to immobilize 10% of available soil N when food supply was limited(Abbott et al.,1981), but when fed with clover litter 6.4% of non-available N was converted into available forms(Barley et al.,1959). These data indicate that earthworms may increase or decrease the availability of N to plants depending on whether or not the system can provide an adequate source of organic N to meet the initial demands of the earthworms. The demand for nitrogen by earthworms is expected to be high since 53-64% of their dry matter composition is protein(French et al.,1957). Earthworms are expected to retain or immobilize amounts of N which are sufficient to meet their own requirements before excreting an excess either in available or unavailable forms. Once organic N is added to the soil earthworms play a significant role in its transformation into readily available forms. Pathways for transformations of N by earthworms include the following:

1. N is assimilated into the biomass of the earthworm. Earthworm bodies readily decompose to release N to plants(Russell, 1910).
2. Mucoprotein secreted through the body wall of the earthworm returns labile N to the soil(Laverack,1963).
3. N is excreted as ammonia through the intestine of the earthworms(Tillinghast,1967). Parle(1963b) found 96% of inorganic N released by earthworms was in the form of NH_3 which upon excretion was rapidly converted to NO_2^-.

The NO_2^- is converted by nitrifying bacteria to plant available NO_3^{--}. An increase in rates of nitrification and amounts of nitrate in earthworm casts has been observed frequently(Parle,1963a,Day 1950;Gupta et al.,1967;Syers et al.,1979).

4. N is secreted as urea through the nephridia of the earthworm(Tillinghast,1967). Once in the soil urea is rapidly converted to ammonia by urease. Syers et al.(1979) found urease activity positively correlated with earthworm activity. The NH_3 resulting from the activity of urease can then pass through the same nitrification pathway as excreted NH_3.

Earthworms also influence nitrogen cycling indirectly by affecting the activity of nitrophilous microorganisms. Some of these effects have been eluded to throughout this literature review. All are summerised and presented in the form of a model(Fig. 3).

Numerous studies have been conducted regarding cropping and cultivation practices and how these influence earthworms. A strong interest has developed in this area recently along with the increased interest in zero and minimum tillage. Soil fauna are considered important in counteracting the compaction and poor infiltration which often accompanies zero tillage(Ehlers,1975;Abbott et

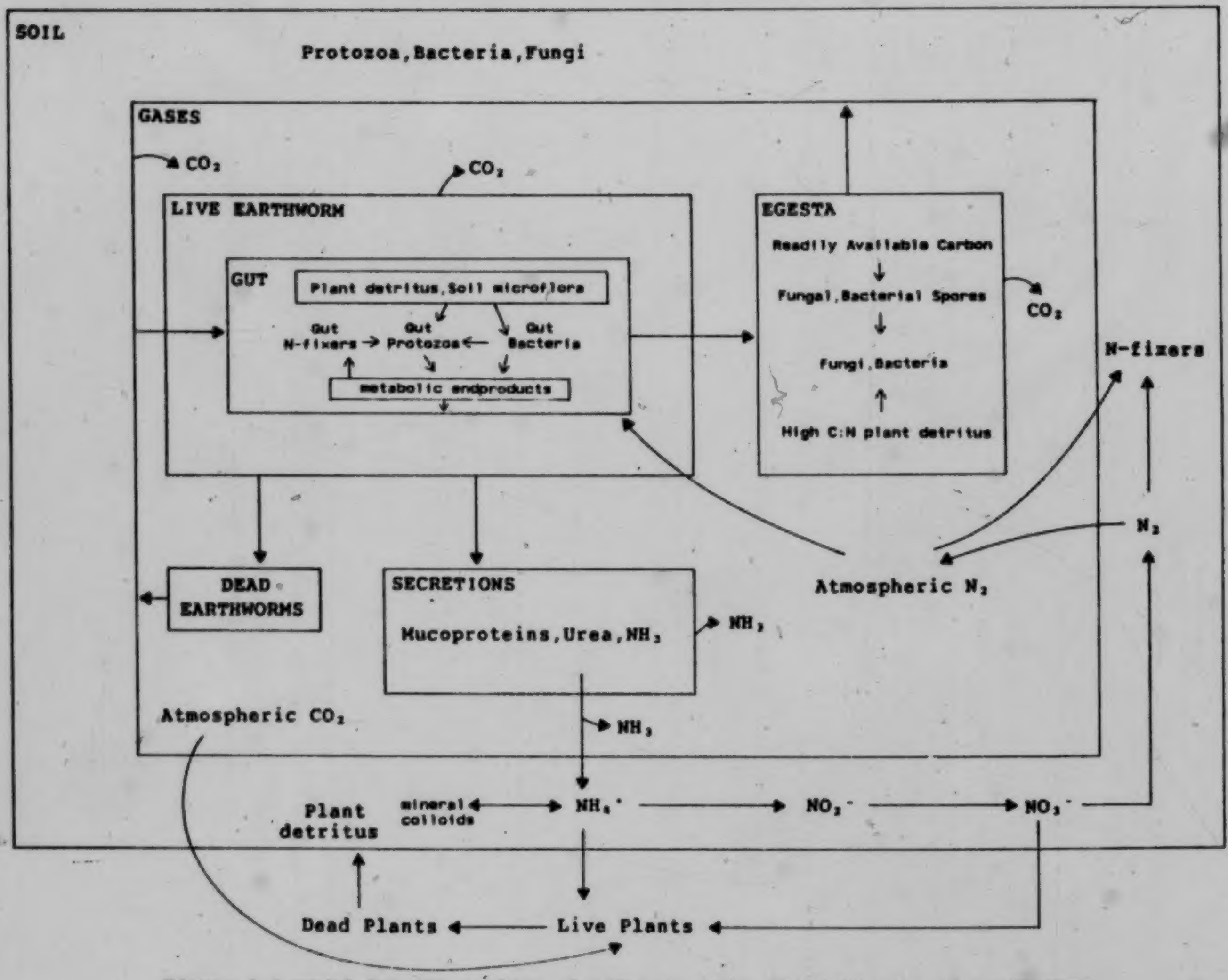

SOIL
Protozoa,Bacteria,Fungi
GASES
CO_2
CO_2
LIVE EARTHWORM
GUT
Plant detritus,Soil microflora
Gut N-fixers
Gut Protozoa
Gut Bacteria
metabolic endproducts
EGESTA
Readily Available Carbon
Fungal,Bacterial Spores
Fungi,Bacteria
High C:N plant detritus
CO_2
N-fixers
N_2
Atmospheric N_2
DEAD EARTHWORMS
SECRETIONS
Mucoproteins,Urea,NH_3
NH_3
NH_3
Atmospheric CO_2
Plant detritus
mineral colloids
NH_4^+
NO_2^-
NO_3^-
Dead Plants
Live Plants

Figure 3:A model for the cycling of nitrogen under the influence of earthworms.

al.,1979). In studies where direct drilling replaced conventional ploughing for periods of 3-4 years, earthworm populations increased 2-6 fold, and earthworm biomass increased 2-3 fold(Edwards and Lofty,1978;Ellis et al.,1977;Barnes et al.,1979;Gerard and Hay,1979). These increases were attributed to reduced mechanical damage and crop residues providing protection from extremes in soil temperature and an additional food supply(Gerard and Hay,1979;Barnes et al.,1979).

After four years of no tillage the number and volume percent of earthworm channels nearly doubled in the Ap horizon, as compared to conventional tillage(Ehlers,1975). These channels were stable to the surface and resulted in significant increases in infiltration rates. In ploughed soils no continuous macropores existed so that no water moved below the Ap(Ehlers,1975). It is felt that direct drilling restricts root growth, especially in the early stages of seedling development(Ellis et al.,1977). Edwards and Lofty(1978) found that once direct drilled soils were inoculated with earthworms, root growth and development approximated that of ploughed soils. The presence of earthworms also resulted in improved germination and establishment of seedlings, and increased growth of the aerial portion of barley plants. On the other hand, Gerard et al.(1979) felt that after six years of direct drilling earthworm activity had not counteracted the effects of high bulk density and low air filled porosity. They did find that in direct drilled soils where earthworm populations increased, the aggregate stability of the soil was greater. It was felt this may have long term positive effects in alleviating the problems associated with high bulk density.

In addition to cultivation practices, the manner in which crop residues are managed affects the structure and dynamics of earthworm populations. Hopp(1947) counted population numbers before and after the first frost under different cropping practices. He found that when a straw mulch was applied to act as an insulating layer a greater number of earthworms survived, and in particular the mature individuals. Individual species, as well as total numbers of earthworms, are affected by cropping practices in different ways. *Helodrilus caliginosa* was present under all types of crop rotations where as *H. parvus* was only found in heavy straw mulch plots and *Diplocardia riparia* occurred in the greatest numbers where sweet clover was used as a surface mulch(Hopp,1947). Barnes et al.(1979) found different cultivation treatments had no unique affect on any single species but the manner in which crop residues were disposed of did. When straw residues were chopped and spread the number of *L. terrestris* increased significantly but when it was burned twice as many *A. chlorotica* were found relative to the mulched treatment.

In non-agricultural ecosystems earthworms have been successfully used as an inoculant to enhance soil development and improve productivity. Stockdill(1979) and Martin and Stockdill(1976) described methods and machinery which can be used to inoculate soils with earthworms.

Huhta(1979) inoculated soils under spruce stands with *A. caliginosa*(mineral soil dweller). This species did not occur naturally in the soils and this was attributed to soil acidity and low palatability of the litter. For this reason soils were also ameliorated with lime, deciduous litter and a combination of both. Three years after inoculation *A. caliginosa* was still present in all the ameliorated plots. Where litter alone was added both the population density and biomass of the earthworms were low and few individuals were found in the mineral soil. Where only lime was added vigorous populations were found, earthworms had penetrated the mineral soil, and some mixing of humus had occurred. It was concluded that, on a practical scale, interplanting with deciduous trees would prove adequate for establishing populations of deep burrowing species in coniferous forest stands(Huhta,1979).

Where topsoil was stripped and removed for other uses earthworms were introduced into the remaining soil to increase productivity(McColl et al.,1982). When soils were inoculated with *A. caliginosa* and planted to ryegrass the earthworm populations flourished. At nine months after inoculation the earthworms were mature and after 14 months 47% of the population was represented by small immatures. Early growth and an increase in dry matter production and nutrient uptake of ryegrass was observed when earthworms were present. McColl et al.(1982) thought these data indicated earthworms could improve productivity of stripped land and suggested keeping reservoirs of earthworms, when stripping, for use in the reclamation process.

Van Rhee(1969a,1969b) inoculated newly drained polders, which were planted to apple orchards, with three species of earthworms. *A. caliginosa* was the best colonizer. It spread at a rate of 6m/year and increased its total population size from 4664 individuals, at the time of inoculation, to about 350,000 in a period of three years. *A. chlorotica* survived well, expanding its population 25-47 fold over the same time span. It spread at a rate of 4m/year. *L. terrestris* did not fare so well and no individuals could be found 1.5 years after inoculation. Van Rhee(1977) concluded at the end of eight years that the earthworms were important in accelerating the breakdown of organic matter and forming a stable crumb structure. Development and growth of orchard tree roots increased in response to the improvement in soil structure. In most plots inoculated with earthworms yields of fruit increased by 6-14%.

Inoculation with earthworms has also been used for reclaiming mine spoils and residues from bauxite refining(Southwell et al.,1982;Vimmerstedt et al.,1973). The residues had an alkaline reaction and were comprised mainly of iron oxides and silica clay. Reclamation entailed covering these residues with a layer of coarse sand and planting with annual rye grass(Southwell et al.,1982). The system was not self sustaining and required repeated fertilization. Inoculation with *E. foetida* proved successful since the earthworms were able to survive and increase nutrient availability to plants. The residues were also used as an ammendment in sandy soils but problems arose with crusting and cementing. Inoculation with *E. foetida* remedied this problem through improving the fertility status and structure of the soil. In Ohio strip mining spoils were reclaimed by planting with hardwood trees. Problems arose when litter from these trees failed to decompose and accumulated(Vimmerstedt et al.,1973). Both calcareous and acid shale spoils were successfully inoculated with *L. terrestris*. Only two years after introduction these earthworms were able to bury or consume 81% of the litter and 43% of the humus which would have otherwise accumulated.

The foregoing provides a few examples where earthworms were utilized or manipulated successfully to solve problems in soil management. Their potential for use in soil management in Alberta and Canada remains largely unexplored. Possibilities which should not be overlooked include:

1. Inoculation into Luvisolic soils in order to improve soil structure and enhance mixing of organic matter into the mineral soil for forest regeneration.
2. Reclamation of spoils from strip mines, open pit mines and tar sands.
3. Utilization in reclamation of fly ash residues, and

aiding in the successful incorporation of fly ash as a soil ameliorant.

3. MATERIALS AND METHODS

3.1 Introduction to the Study

In some respects it would have been desireable to culture earthworms used in this study under field conditions. However, given the lack of knowledge regarding survival of earthworms after inoculation as well as the time constraints involved, it was decided a laboratory study would suffice to meet the previously stated objectives. This approach permitted the earthworms to be active in the soil for a longer time period than seasonal restrictions would allow in the field. Furthermore, in the laboratory setting environmental conditions such as soil moisture and temperature, daylength and light intensity, known to affect the behaviour and activity of earthworms, could be monitored and in some cases controlled allowing better control of variability introduced by these factors. The utilization of transparent plexiglass cylinders allowed observation of the behaviour of the earthworms below the soil surface which could not be so easily accomplished in the field.

3.2 Selection of Soils

In order to accomodate the primary objectives of the study it was felt that the soil materials used should meet three basic requirements.

1. They should be essentially devoid of pedological structural development.
2. They should possess qualities representing a broad range in dominance of particle size.
3. While maintaining the integrity of the above two the materials selected should, to the greatest extent possible, be free of those qualities known to affect the activity of earthworms adversely.

In light of the above, it was decided that undisturbed, calcareous, parent or C horizon material would best meet the requirements of this study. Lack of structural development in the materials allowed for the observation of structural features resulting from the activity of the earthworms. Inherently low in organic matter, the chosen material was also ideal for studying the interaction between the organic and inorganic fractions of the soil, as might be influenced by the earthworms. Utilization of the laboratory approach to the study allowed control or monitoring of most soil conditions implicated in controlling the activity of earthworms with the exception of soil reaction. The selection of calcareous parent material ensured an environment of moderate reaction within the range, considered in the literature, optimal for the activity of earthworms(Reynolds,1977).

Three soil parent materials were chosen, all were calcareous and each exhibited a different particle size distribution. The first, hereafter referred to as Spruce Grove, is of a pitted deltaic origin and possesses a dominance of fine sand particles. The second, hereafter referred to as Cooking Lake, is of a morainal till origin and exhibits a fairly uniform distribution of particle sizes, while the third, of lacustrine origin dominated by silt particles, is referred to as Ellerslie. The names attached to these soil materials refer, in a general way, to the location of the site where the samples were collected and should not, in any way, be considered as a classification of the pedons associated with the parent materials. Particle size analysis of samples taken from bulk soil collection are given in Table 5.

Table 5. Particle size analysis for Spruce Grove, Cooking Lake and Ellerslie parent materials

Soil Material	%Sand	%Silt	%Clay	Textural Designation
Spruce Grove	84.4±.3	6.1±1.2	9.5±1.5	SL
Cooking Lake	35.1±.1	29.6± .1	35.3± .3	CL
Ellerslie	8.6± 0	58.4± .6	33.0± .4	SiCL

All soil samples were collected in the vicinity of the city of Edmonton. As well as collecting bulk samples of each, bulk density cores were also taken using a Uhlander bulk density core sampler. Bulk samples were air dried, ground to pass a 2 mm. sieve and stored in air tight containers for future use. Bulk density cores were collected in the field, wrapped in plastic bags and stored in cardboard containers until needed.

3.3 Selection of Food

As discussed earlier in the 'Literature Review' only limited and conflicting information regarding the feeding preferences of various earthworm species is available. The majority of these studies have been conducted with deciduous tree litter where the ultimate objective was to utilize the results to discern distribution and function of earthworms in a natural environment. For the purposes of this study it was deemed appropriate to use common lawn grass since it is vascular in nature and not considered repugnant to earthworms. Preliminary experimentation proved this premise to be true and bulk collection of the grass proceeded. A single collection from a site known to be free of contaminants provided sufficient material for the duration of the study. The bulk grass collected was oven dried(60°C) and stored in air tight bags for later use.

3.4 Selection of Earthworms

All earthworms do not behave or function ecologically in a uniform manner(Reynolds,1977). For this reason species of earthworms from two distinctly different ecological groups were selected for this study. *Lumbricus* *terrestris*(Linnaeus) was chosen from the anecique group as defined by Phillipson et al.(1976). Its most distinctive behavioural patterns include the construction of permanent burrowing systems and the collection and withdrawal of litter from the soil surface for transport to great depths. Because of its characteristic nocturnal behaviour it is commonly referred to as the "nightcrawler" or "dewworm". The second group of earthworms was chosen from the endogie group(Phillipson et al.,1976). This group constructs non-permanent channels and their activity is normally limited to the top 10-20 cm of the soil. From this group the species *Octolasion tyrtaeum*(Savigny) and *Aporrectodea turgida*(Eisen) were chosen for this study. Individuals representing the species used are shown in Plate 1.

The earthworms were collected from an area within the city limits of Calgary known to have large populations of *L. terrestris*. After collection they were stored in a cooler full of moist soil and quickly transferred back to the laboratory. Once in the laboratory individuals of *L. terrestris* were sorted out and stored in a large plastic garbage can filled with a mixture of peat moss and mineral soil. The container was covered with a fine net to allow free circulation of air and prevent the escape of the earthworms. Individuals of *O. tyrtaeum* and *A. turgida* were stored in a similar manner using a smaller container. Both containers were maintained at a temperature of about 10°C.

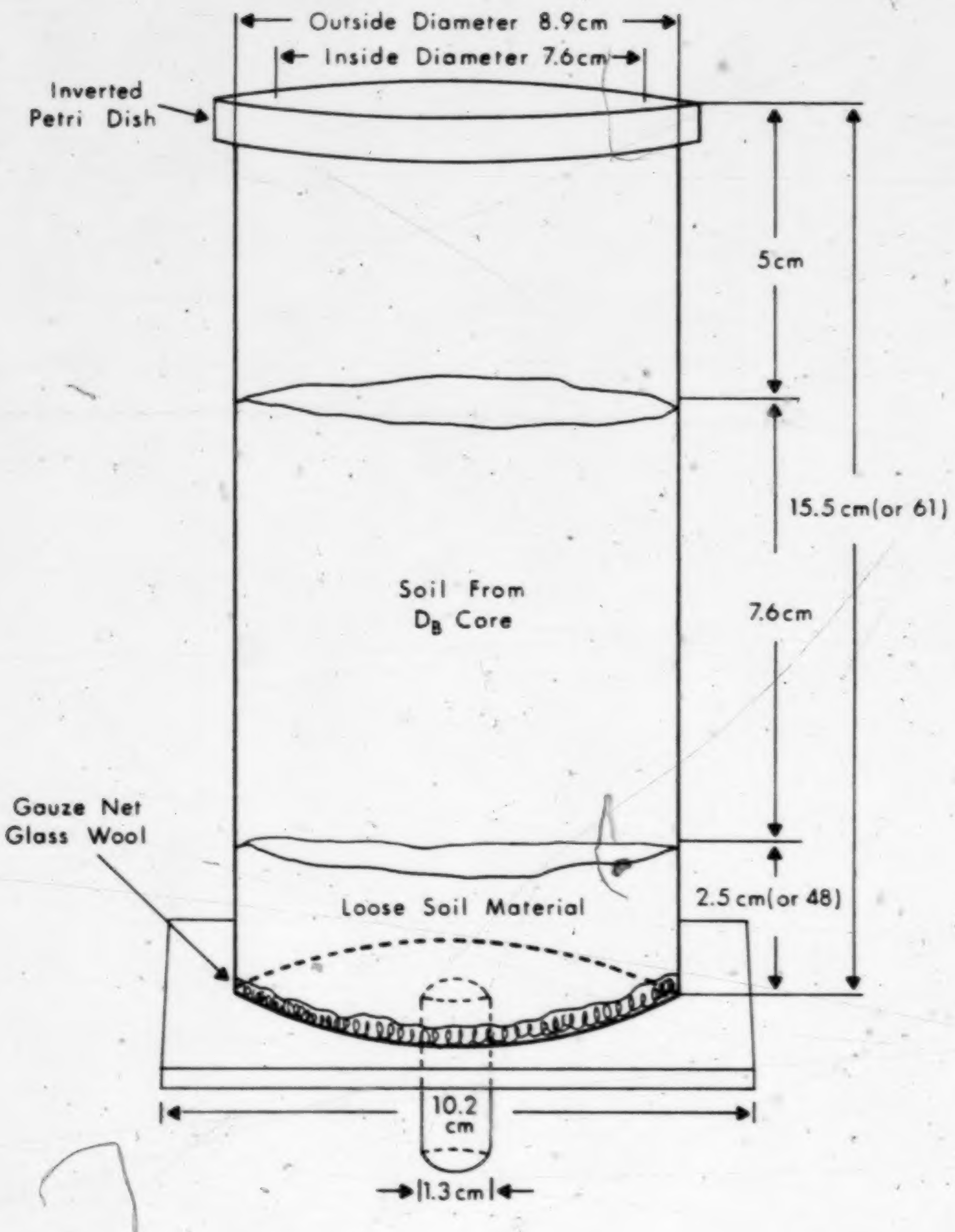
Plate 1:Individuals representing the species used in this study.(left to right) *Octolasion tyrtaeum* (1 specimen), *Aporrectodea turgida* (1 specimen) and *Lumbricus terrestris*(2 specimens).

A subsample of these earthworms was preserved according to the procedure described by Fender(1982-Appendix I) and sent to Dr. Valin Marshall at the Pacific Forest Research Station in Victoria, B.C. for identification. The results from his work are shown in Appendix II.

3.5 Experimental Design

The experiment was conducted in a cold room where earthworms were housed in plexiglass cylinders. Appropriate control were included in the experimental design. Room temperature was maintained at approximately 10°C. Light bulbs(60 watts) were attached to shelves above the columns and their height adjusted to provide 40-70 ft.c. at the surface of the columns. The lighting system was controlled by a timing device to provide a 14:10 hour day/night cycle similar to that suggested by Tomlin(1977).

The cylinders, as shown in Fig. 4, were constructed of plexiglass tubing with a drainage outlet provided at the base. A centrally located opening was located on the side of the tubing to allow access for a soil moisture cell(obtained from SOILTEST,INC.) to be used for monitoring soil moisture and temperature. All soil moisture cells had been previously calibrated in the same type of soil material that would be monitored during the experiment. Cylinders used for the controls and endogie species of earthworms were 25 cm in height, while those housing the individuals of *L. terrestris* were 60 cm in height; the latter being taller in order to



Outside Diameter 8.9cm
Inside Diameter 7.6cm
Inverted Petri Dish
5cm
15.5 cm(or 61)
Soil From D_B Core
7.6cm
Gauze Net Glass Wool
Loose Soil Material
2.5 cm(or 48)
10.2 cm
1.3 cm

Figure 4:Design and specifications for plexiglass columns.

accomodate the earthworms deep burrowing habit.

In order to pack the cylinders with soil a circle of mesh screening was first placed in the bottom of the cylinder to prevent escape of the earthworms. A mat of fibreglass wool was placed over the screen allowing the leachates to filter through but preventing the soil material from passing through the drainage outlet. Bulk soil, ground to pass a 2 mm. sieve, was added to the cylinders through a long necked funnel with constant shaking in order to achieve an even packing. When the level of the soil was even with the moisture cell opening, the cell was placed vertically into the soil, the wires were fed through the access hole to the outside of the cylinder and the access hole was sealed off with caulking. The remainder of the cylinder was then filled with soil, to about 15 cm from the surface in order to provide sufficient space for the addition of the undisturbed soil core, and eventually the addition of grass. Once the soil cores were placed in position packing was completed, and the cylinders were transferred to a basin of distilled water. The cylinders remained in the basin until fully saturated from the bottom up. They were then removed and allowed to drain freely before any addition of earthworms.

Before the earthworms were transferred from the storage containers into the cylinders, they were placed in smaller containers holding soil material corresponding to that found in the cylinders into which they would eventually would be placed. After a period of two days the earthworms had expelled the soil material from their gut that was retained from the storage containers and were ready for transfer into the cylinders. Once the earthworms were in the columns an inverted plastic petri dish was used to cover the top of the column to prevent their escape. A black cover was placed around the cylinders in order to simulate subsoil lighting conditions.

Five treatments for each of the three soil materials collected, were randomly assigned in triplicate as follows;

Treatment 1:Soil + grass
Treatment 2:Soil + *O. tyrtaeum* + *A. turgida* + grass
Treatment 3:Soil + *L. terrestris* + grass
Treatment 4:Treatment 2 + *L. terrestris*
Treatment 5:Soil alone

Thus 15 columns were set up for each soil material, giving a total of 45 columns for the experiment. Soil moisture cells were included in only one of the three replicates for each treatment.

Results from soil moisture and temperature readings taken at two week intervals are found in Appendix III. Details regarding the numbers, weight and species of earthworms as well as amounts of soil added to each column are itemized in Appendix IV. Through the duration of the experiment some earthworms escaped or, as in the case of the

Ellerslie soil, had difficulty adapting and died. Dead earthworms were removed from the columns and replaced with live ones. These additions and removals are itemized in Appendix V.

Through preliminary experimentation it was determined that the addition of 0.5 gm.(O.D. Basis) of grass to the columns on a monthly basis would provide adequate substrate for the earthworms. Thus 0.5 grams of grass was added to treatments 1-4, every month for the duration of the experiment.

The original intention of the study was to allow the earthworms to work the soil for a period of one year. Unfortunately a malfunction in the cooling unit resulted in temperatures rising to the point where all the earthworms died. For this reason data were collected for a period of 8,10 and 11 months for the Ellerslie, Cooking Lake and Spruce Grove soils respectively.

3.6 Leachate Samples

Leachates were collected from all the columns at one month intervals for the duration of the experiment. In order to prepare the cylinders for the leachate study 7.5 cm diameter # 41 Whatman filter papers were placed on the surface of the soil columns in order to prevent disruption of the grass and/or soil by infiltrating water. 50 ml of distilled water were added to the top of each of the columns and collected at the drainage outlet. After collection the leachates were filtered through 0.2 millipore filters to remove colloidal material. This step was felt necessary to prevent interference with future analysis. The filtrates were transferred into autoclaved nalgene bottles and stored at $^{-}$4°C. Poor hydraulic conductivity through the columns containing Ellerslie soil caused difficulty in collecting leachates. Saturation of the soil with water resulted in reducing conditions and the presence of gley which appeared to affect the activity of the earthworms deleteriously and in some cases caused their death. Consequently, by the second sampling period, a light vacuum($\leq$1/3 bar-monitored using a vacuum gauge) was applied to the bottom of the columns in order to withdraw the leachate. This approach appeared to be successful in removing excess water from the soil and was used for several ensuing sampling intervals. Unfortunately by the end of the fifth sampling period repeated application of the vacuum had resulted in compaction of the soil and this further reduced hydraulic conductivity. The tension of vacuum required to remove water at this stage would have been too great a stress on the earthworms. As a result subsequent sampling from these columns was halted until the termination of the experiment. Thus leachates were collected for a period of 8,10 and 11 months for the Ellerslie, Cooking Lake and Spruce Grove columns respectively.

Chemical analyses of the leachates included the determination of pH, concentrations of Ca, Mg, Na, and

K(using ICP emission spectroscopy) and concentrations of soluble total and inorganic carbon(using a Beckman IR Soluble Carbon Analyzer).

After preliminary analysis it was concluded that bulking of samples was justified since differences in chemical composition of the leachates collected monthly were moderate. Thus final chemical analyses were performed on leachates collected monthly but bulked to represent bimonthly intervals.

3.7 Soil Samples

After the experiment was terminated all of the soil columns were transferred to a cold room and stored at ⁻4°C in order to prevent chemical deterioration of the samples. Two replicates from each treatment were selected for chemical analyses while the third was used for impregnation and the preparation of thin sections. Samples chosen for chemical analyses were taken out of cold storage, the plexiglass cylinders removed, and the soil carefully dissected and separated into faecal pellets, tunnel linings, and soil material which had apparently not passed through the earthworms' gut. Soil materials that were in contact with dead earthworms, and the dead earthworms themselves, were completely disposed of to eliminate the possibility of erroneous results(especially for total N) because of contamination from the bodies of the earthworms. The samples were air dried, ground to pass a 2 mm. sieve and stored in air tight jars. Sub-samples used to determine total carbon, total inorganic carbon and total N were further ground to pass a 100 mesh sieve.

3.7.1 Chemical Analyses

3.7.1.1 pH

pH was determined in 0.01M $CaCl_2$ according to McKeague(1978).

3.7.1.2 Exchangeable Cations

Exchangeable cations were extracted with 1N NH_4OAc using centrifugation according to Thomas(1982). Concentrations of metallic cations were determined using a Perkin Elmer 303 atomic absorption spectrometer.

3.7.1.3 Total Exchange Capacity

Total exchange capacity was determined by NaOAc saturation(McKeague,1978). The concentration of exchangeable Na was determined on a Perkin Elmer 303 atomic absorption spectrometer.

3.7.1.4 Carbon Analysis

Total Carbon was determined by dry combustion using a Leco Carbon Determinator(Model CR12).

Inorganic Carbon was determined according to Bundy and Bremner(1972).

Organic Carbon was derived by subtraction of inorganic carbon from total carbon.

3.7.1.5 Total Nitrogen

Samples(approximately .5gm.) were digested in a Kjeldahl apparatus using calpak(K_2SO_4-$CuSO_4$) as an oxidizing agent and catalyst. Total N was determined as NH_4^+ through the formation of an ammonia-salicylate complex. Concentrations were determined colorimetrically at a wavelength of 660nm. on a Technicon Autoanalyzer(Industrial Method No. 334-74 W/B⁺-Technicon Autoanalyzer II).

3.7.1.6 Neutral Sugars/Uronic Acids

Colorimetric Determination of Neutral Sugars

Doutre et al.(1978) compared both the anthrone and phenol sulphuric acid methods to results obtained using gas liquid chromatography(GLC) for determination of aldoses. They found that results from the phenol sulphuric acid method were comparable to those from GLC provided interfering cations and anions were first removed. Conversely the rate of color development and fading using anthrone was highly temperature- and time-dependent and results were low compared to GLC. Dubois et al.(1956) suggested that measurement of sugars using anthrone may be limited to free sugars and glycosides while the phenol sulphuric acid method may be more suitable for a broader range of sugars including their methyl derivatives, oligosaccharides and polysaccharides.

In this study it was most desireable to determine sugars as a general group rather than specific kinds. The phenol sulphuric acid method was chosen, as described by Dubois et al.(1956), because it reacts with a broader range of sugars and produces a more stable color than the anthrone determination. D-galactose was used as a synthetic standard. Absorbance was read at a wavelength of 490 nm on a Pye Unicam SP1800 spectrophotometer.

Colorimetric Determination of Uronic Acids

The use of carbazole is the most common colorimetric method for the determination of uronic acids. The procedure described by Bitter and Muir(1962) was used in this study. Reproducability and reliability of results were greatly improved by freezing the test tubes and the Na-tetraborate-sulphuric acid reagent in an acetone bath(-70°C) prior to layering the sample on top of the reagent. Galacturonic acid monohydrate was used as a synthetic standard as recommended by McGrath(1971). Absorbance was read at a wavelength of 530 nm on a Pye Unicam SP1800 spectrophotometer.

Removal of Metallic Cation Interferences

The colorimetric techniques used for both neutral sugar and uronic acid determinations require the removal of metallic cations, especially iron (Doutre et al.,1978;McGrath,1971). Dormaar and Lynch(1962) stated that large amounts of iron released through hydrolysis and alkali extraction could not be removed adequately stannous chloride reduction. After assessing various techniques for Fe removal they concluded that removal through ion exchange was the only feasible approach. For this purpose Amberlite IR-120 exchange resin(H^+ form) was used.

Separation of Neutral Sugars and Uronic Acids

To analyze for uronic acids properly they must be separated from aldoses in order to avoid interference during the colorimetric determination (Greenland et al.,1975). This was accomplished using Amberlite IRA-400 exchange resin. The exchange resin was purchased in the chloride form and converted to the acetate form by leaching with 1N NaOAc as recommended by Thomas and Lynch(1961). They found that the acetate form, but not the chloride form, permitted separation of mixtures after hydrolysis without neutralization.

Ion Exchange Columns

Pyrex open ended burettes of 42 cm height and 1 cm diameter were used as chromatographic columns. Rubber tubing was attached to the bottom of the burette and a screw clamp was used to control the flow rate. Glass wool was placed in the bottom of the burrette in order to prevent the resin from flowing out. A slurry of the resin was poured into the burette to a height of 30 cm. A rubber stopper, through which a glass rod was inserted, was placed into the top of the burrette. A length of tygon tubing was attached to the outer portion of the glass rod to complete a siphon system. This system permitted the entry of either sample or regenerating solution. Utilizing a siphon system increased the overall efficiency of the analysis such that 16 cation and 16 anion exchange columns could be set up and monitored simultaneously.

Elution of Hydrolyzates

Cation Exchange Columns(Amberlite IR-120)

5 ml of hydrolyzate was transferred into a test tube and diluted to 15 ml with distilled water. A 150 ml beaker was placed under the column and the screw clamp adjusted to set the flow rate of the siphon at 1 drop/3 seconds. The diluted hydrolyzate was then completely siphoned into the column. The test tube was rinsed down twice with distilled water where each rinsing was allowed to be completely siphoned into the chromatographic column. To complete the elution of the hydrolyzate, distilled water was siphoned through the column until 100 ml

of effluent was collected in the beaker under the column.

Anion Exchange Columns(Amberlite IRA-400)

Elution of samples through the anion exchange column was a two step procedure for separation of neutral sugars(eluted with distilled water) from uronic acids(eluted with 1N H_2SO_4). Routinely this process would require that only an aliquot from the cation exchange column effluent be eluted through the anion exchange column. Since concentrations of both substances to be analyzed were very low, the entire 100 ml of effluent was immediately siphoned through the anion exchange column. A 300 ml beaker was placed beneath the outlet of the column and the flow rate adjusted to 1 drop/3 seconds. The 150 ml beaker was rinsed twice with distilled water. Each rinsing was allowed to siphon completely through the column. Distilled water was siphoned through the column until 300 ml of effluent had been collected in the beaker positioned under the exchange column. Once full, the beaker was transferred onto a sand bath (40°C) and allowed to evaporate down to less than 25 ml. The concentrated solution was quantitatively transferred into a 25 ml volumetric flask and made up to volume with distilled water. Subsequently a 1 ml aliquot from this volume was used to determine the concentration of uronic acids, by the carbazole method described earlier.

Regeneration of the Exchange Columns

16 cation and anion exchange columns could be easily and simultaneously regenerated by using a manifold system to transport the regenerating solution (gravity fed) from a carboy through the manifold outlets attached to the lengths of tygon tubing. The regenerating solution then simply flows out of the bottom of the columns into a drain. This manifold system served to regenerate the columns with little supervision(Fig. 5).

Cation exchange columns were regenerated with 6N HCl until the effluent was colorless and free of Fe(Doutre et al.,1978). With the size of columns used anywhere from 100 to 300 ml of acid were required. Once regenerated the columns were further leached with distilled water until the spot test for $Cl^-(AgNO_3)$ was negative(Doutre et al.,1978). Columns were regenerated at their inception and after each sample had been eluted. The columns were repacked after 8-10 cycles since their continual re-use resulted in compaction and degradation of the resin.

Anion exchange columns were regenerated by flushing the columns first with distilled water to remove excess acid and then with 1N NaOAc until a negative spot test for $SO_4^{--}(BaCl_2)$ was attained(Doutre et al.,1978). Subsequently the

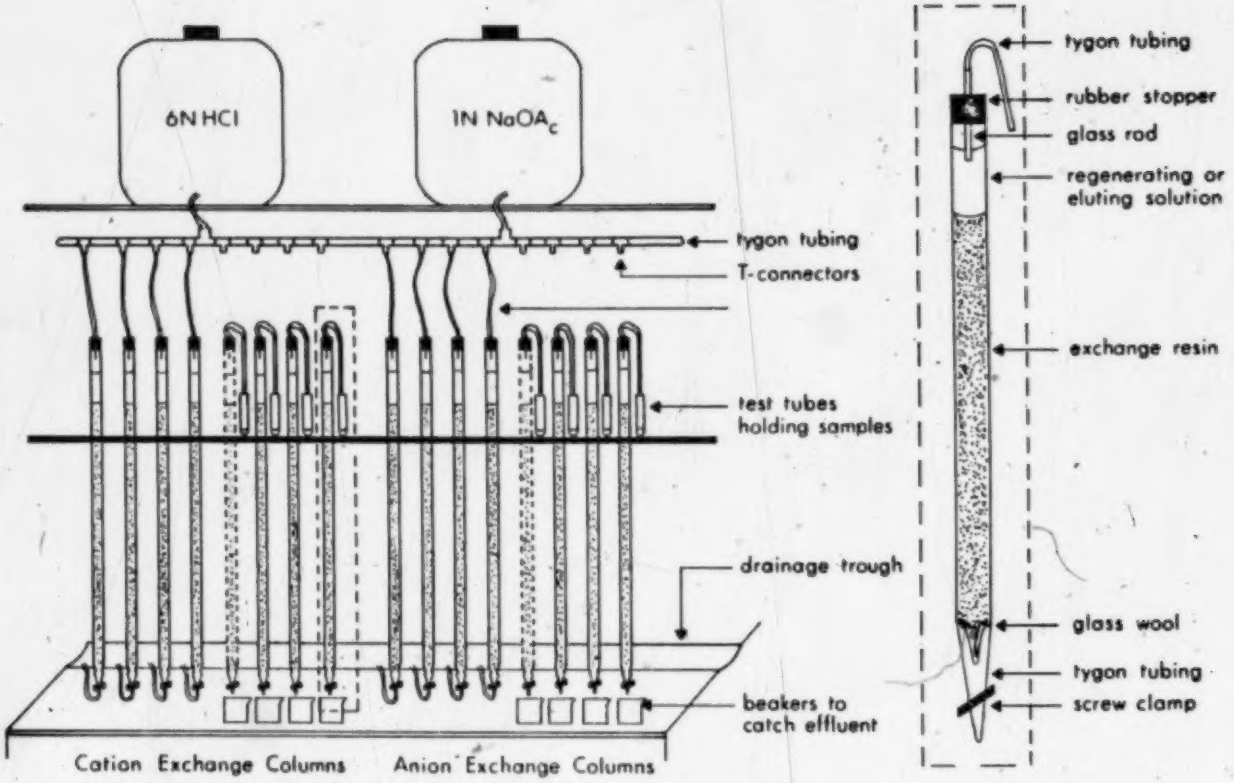

6N HCl
1N $NaOA_c$
tygon tubing
T-connectors
test tubes holding samples
drainage trough
beakers to catch effluent
Cation Exchange Columns
Anion Exchange Columns
tygon tubing
rubber stopper
glass rod
regenerating or eluting solution
exchange resin
glass wool
tygon tubing
screw clamp

Figure 5: Manifold system used to facilitate entry of samples or regenerating solution.

columns were leached with excess distilled water to remove the excess NaOAc. These columns were also regenerated at their inception and after each sample had been eluted. This resin, especially in the acetate form, degenerated and compacted much more rapidly than the cation exchange resin and required repacking after every 4 to 5 cycles.

Extraction and Hydrolysis

Numerous approaches to extraction and hydrolysis for the study of organic compounds in soil exist. Many of these have been discussed in review articles such as those by Cheshire(1979) and Greenland et al.(1975). Generally the approaches use organic solvents for extraction or are constituted by a single alkaline or acid hydrolysis. In this study it was preferred to use a stepwise extraction where sugars and uronic acids could be separated into a free or weakly organic bound fraction, a clay bound fraction, and a residual fraction. For this reason the extraction procedure described by Anderson et al.(1974) was chosen and modified in this study to accomodate a smaller sample size. Once obtained, all extracts were hydrolyzed in 3N H_2SO_4 at 121°C and 15 p.s.i. for one hour(Dormaar et al.,1962). The hydrolyzates were filtered through GF/A glass microfibre filters, and the filtrate made up to volume with distilled water in 50 ml flasks. A

5 ml aliquot from this volume was used for subsequent ion exchange chromatography and quantification of sugars and uronic acids.

Standard addition experiments using soil extracts, where the standard was added prior to hydrolysis, were done for all extracts including .01N HCl which was discarded in the original extraction process of Anderson et al.(1974). Recoveries from standard addition experiments for sugars were considered acceptable and in line with those reported by McGrath(1971) with the exception of the NaOH-Na$_4$P$_2$O$_7$ extraction where blanks were unusually high and recoveries low. Although some attempts were made to determine the reason for these poor recoveries none could be considered truely successful. Further investigation into this problem was not considered to be within the scope of this study. Therefore a .5N NaOH extraction like that used by Dormaar and Lynch(1962) was substituted for the NaOH-Na$_4$P$_2$O$_7$. This proved successful. Recoveries for uronic acids ranged from 41-47%, in line with those reported by McGrath(1971). Although McGrath(1971) suggested the use of a correction factor to make up for the losses of uronic acids that resulted from hydrolysis it was not deemed necessary for this study.

Once the standard addition experiments were completed, analysis of the soil samples from the cylinders were undertaken. After all the faecal pellet samples and one half of the tunnel lining and soil samples had been extracted and analyzed, no sugars were detected in the .01N HCl extract and no uronic acids were found in any of the extracts. For this reason the .01N HCl extract was disposed of and the uronic acid analysis aborted for the remainder of the samples to be analyzed.

3.7.2 Microbiological Analyses

Preliminary experiments in microbiology were conducted to determine the areas of study which would be most valuable to pursue in detail. Serial dilutions in sterile water were made using Spruce Grove samples from both control columns and faecal pellets of *L. terrestris*. Aliquots of 0.1ml size were transferred onto PCA [1] plates to produce a dilution series that ranged from 10^{-1} to 10^{-7}. Aliquots were also transferred, using pasteur pipettes, into broths of Lactose, FVM, Butlins and M77. Both plates and broths were incubated for one week at room temperature before observations and counts were made.

At the end of the incubation period counts were higher on the PCA plates from the faecal pellets as compared to the control. As well, an enrichment of large, yellow colored colonies was observed on the faecal pellet plates. Several of these colonies were isolated, transferred onto #1 and Skim Milk plates and observed under a phase-contrast microscope. The colonies were concluded to belong to the genus *Cytophaga* for the following reasons.

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[1] Recipes for all plate and broth media are found in Appendix VI.

1. They exhibited a spreading growth form on the #1 media.
2. They demonstrated lytic capability against protein(Skim Milk plates).
3. They produced pungent aromas.
4. They were observed as large motile rounded-rod shaped organisms under the phase contrast microscope.

After considering these observations a more detailed experiment to investigate organism numbers and lytic activity of the *Cytophaga* began. Serial dilutions for the control soil, endogie faecal pellets, and *L. terrestris* faecal pellets from all three soils were made. Aliquots of 0.1ml size were transferred onto PCA plates in duplicate for enumeration of *Cytophaga*, bacteria and actinomycetes, and similarly onto Rose Bengal plates for enumeration of fungi and yeast. The plates were incubated at room temperature for 7 days before the counts were made.

After the counts were completed 21 colonies of *Cytophaga* were isolated and assayed for lytic activity against protein(Skim Milk Agar), mannan(Yeast Agar), cellulose(Butlins Broth + cellulose strips), other bacteria(Bacterial Agar) and chitin.

Three approaches were taken to assay for lytic activity against chitin.

1. Pulverized mushrooms were mixed in a 1.5% agar solution which was sterilized and poured into plates.
2. Chitin suspension plates were prepared using a commercial chitin which was finely ground, mixed in a 1.5% agar solution, sterilized and poured into plates.
3. Hydrolyzed chitin plates were made according to Gray and Bell(1962).

Initially the pulverized mushroom medium was unsuccessful since the plates dried out quickly before the colonies could become established. Another set of plates were used where a film of water agar was poured overtop of the mushroom agar. This proved successful.

Selected colonies were also assayed for their ability to attack the cellular structure of other bacteria. Cultures of bacteria were grown and made into plates after mixing in a 1.5% solution of agar and sterilization. Problems similar to those with the mushroom agar were encountered where the plates dried out before any reliable observations could be made, although in some cases lytic activity was observed.

At the end of the first incubation period cultures from the lactose and FVM broths were transferred into fresh media and allowed to incubate for one additional week. At this time the cultures were transferred into septum vials and assayed for acetylene reduction. Results from these assays proved negative. Cultures from the FVM broths were observed under the phase contrast microscope. Although spirillum-like organisms were observed in the cultures the omnipresence of protozoa in the cultures from the faecal pellet samples were considered so problematic as to halt further study in the area of dinitrogen fixation in the faecal pellet samples. At a later data tunnel lining samples were assayed similarly in FVM broth in order to avoid problems with the protozoa.

No evidence of butyric acid production was observed in the flasks of M77 in the preliminary experiment. Bhat(1974) claimed that earthworms caused "Azotobacterization" of soils. Recognizing the possibility that the negative result obtained could be specific to the samples used a more extensive experiment was set up using the serial dilution already prepared for total plate counts.

The lowest dilution(10^{-1}) from the faecal pellet samples was the only one to show a positive reaction in the Butlins broth during the preliminary experiment. In view of the possibility that anaerobic organisms may be present in greater numbers in the faecal pellet samples an MPN experiment using the same medium, was set up. Again the serial dilutions used were those already prepared for the total plate counts.

3.7.3 Particle Size Analysis

Particle size distribution was determined for selected samples. The <2um fraction was collected by gravity separation(Jackson,1975), dried at 105°C and weighed. The sand fraction was collected by washing the remainder of the sample through a 300 mesh sieve. This fraction was also dried at 105°C and weighed. Silt was determined by subtraction.

After the weight of the <2um fraction was determined this fraction was treated with H_2O_2 and heated to remove colloidal organic matter, dried and weighed. This approach was used to determine what percentage of the colloidal fraction was organic versus inorganic.

3.7.4 Microscopy

One 7.5 x 5 cm thin section(32um) for each treatment was prepared using Scotchcast epoxy resin for impregnation. Selected samples of soil, faecal material and earthworms were prepared for examination on a Cambridge Stereoscan S 4 scanning electron microscope. Earthworms were transferred through numerous solutions of ethanol with concentrations increasing from 70-95% before critical point drying.

3.7.5 XRD Analyses

Samples of faecal pellets from Treatments 2-4 and the corresponding control, from all three soils were prepared for XRD analyses. The clay fraction was collected from the samples by gravity separation(Jackson,1975). Slides of Ca^{++} and K^{+} saturated clays were prepared by mounting on glass slides by the paste method(Theisen and Howard,1962). X-ray diffraction analyses were performed with a Phillips diffractometer and Cu-K-α radiation, with six pretreatments as follows:

1. Ca-saturated, 54% relative humidity.
2. Ca-saturated, ethylene glycol solvated.
3. K-saturated, 105°, 0% relative humidity.
4. K-saturated, 54% relative humidity.
5. K-saturated, 300°C, and
6. K-saturated, 550°C.

A similar X-ray analysis was done on samples treated with H_2O_2 to remove organic matter.

3.8 Grass Samples

After the soil columns were removed from cold storage and dissected the grass on the surface of the columns was collected, washed to remove mineral soil material, oven dried(60°C) and weighed. Only those samples from treatments 1 and 2 were chemically analyzed. Those from treatments 3 and 4 were not large enough to allow a proper analysis. The samples from treatments 1 and 2 were further sub-divided into three sections(top,middle,bottom) in accordance with the increasing degree of decomposition from top to bottom. These samples were ground to pass a 100 mesh sieve and digested according to Parkinson et al.(1975). Concentrations of Ca, Mg, Na and K were determined by ICP emission spectroscopy, while total N was determined using steam distillation(McKeague,1978).

3.9 Statistical Analyses

Data were analyzed by analysis of variance(ANOVA) procedures using the University of Alberta public library APL programs. Factors were judged significant when F ratios exceeded the 5% probability level. Four ANOVA models were used depending upon the type of data under consideration.

Final measurements of unaltered soil chemical properties were analyzed as a 3x5 factorial experiment with soil type at three levels and treatments at five levels. Chemical elements in the grass recovered from Treatments 1 and 2 at the termination of the experiment were analyzed as a 3x2 factorial. Treatment effects in leachate analyses were evaluated by one-way ANOVA's from a given soil at a given leaching time for all treatments and for a given treatment and soil over time. Quantitative comparisons of leachates across soil types were not done. Chemical data for the parts dissected from the columns(tunnel linings,faecal pellets,unaltered soil) were analyzed using a split-plot design where the whole plot was a 2^3 factorial with soil type and treatment at three levels and the dissected part was the split-plot factor.

Where significant F tests occurred means were compared by the Student-Newman-Keuls procedure at the 0.05 significance level.

4. RESULTS AND DISCUSSION

4.1 Introduction

The results and discussion for this study are presented together in this chapter. The chapter is divided into three parts which essentially correspond to the objectives set out in Chapter 1.

The first part includes information relevant to the topic of earthworms and the development of soil structure. It has two sub-sections which fundamentally correspond to the two primary objectives. The first sub-section includes results from the micromorphology along with a discussion of earthworms and their role in the formation of soil structure. This sub-section also includes results relevant to the third secondary objective; changes in soil porosity as influenced by earthworms. The second sub-section relates to the topic of earthworms and the stabilization of soil structure. It includes pertinent results from soil chemical, physical and microbiological analyses.

The second part of this chapter includes the results and discussion relevant to the topic of earthworms and their influence on microorganisms and decomposition.

The third part of this chapter corresponds to the first of the secondary objectives and presents data, primarily for the chemical analysis of the grass, soils and leachates, related to the topic of earthworms and nutrient cycling.

4.2 Earthworms and the Development of Soil Structure

Brewer(1976) defined soil structure as follows,

> "The physical constitution of a soil material as expressed by the size, shape and arrangement of the solid particles and voids, including both the primary particles to form compound particles and the compound particles themselves."

Allison(1968) emphasized the importance of understanding that good granular structure involves two separate forces. Those resulting in aggregate formation and those enhancing stability. He defined aggregate formation as follows,

> "Primarily orientation of fine soil particles bringing them so close together that the physical forces hold them firmly together when allowed to dry."

Stabilization involves conditions outside the aggregate as well as within, requiring the forces within, which tend to hold the aggregate together, to be greater than the forces which tend to pull them apart. Allison(1968) defined aggregation as follows,

> "a naturally occurring cluster or grouping of soil particles in which the forces holding the particles together are much stronger than forces between adjacent aggregates."

Good soil structure is not only characterized by aggregation but also aeration porosity(Baver,1968). Aeration porosity refers to the largest pores which increase in size along with an increase in aggregation and aggregate size. The optimal 20-30% porosity is achieved with aggregates ranging from 2-3 mm. in diameter(Baver,1968).

Thus, three components should be considered in evaluating the development of soil structure - formation, stabilization and porosity. The following results and their discussion are presented in two sections. The first concentrates on the aspects of formation of soil structure and porosity while the second focuses on processes involved in stabilization.

4.2.1 Earthworms and the Formation of Soil Structure

4.2.1.1 Introduction

In this study micromorphological descriptions of thin sections of soil facilitated the study of the formation of soil structure. Traditional approaches to studying soil structure have usually been of a destructive nature(wet or dry sieving) or of an indirect nature(pore size distribution and pore volume). Both of these approaches, although useful, provide no information regarding the elements of arrangement and shape in the definition of soil structure. In addition they are usually limited to assessments at the higher levels of organization. The micromorphological approach facilitates a direct means of describing the arrangement of soil components over a wide range of organizational levels. Soil fabric deals with the arrangement of constituents and is defined by Brewer(1976) as follows,

> "the physical constitution of a soil material as expressed by the spatial arrangement of the solid particles and associated voids"

In the past micromorphology has been used to study the influence of soil fauna, including earthworms, on the development of soil fabrics(Babel, 1968,1975;Pawluk, 1980;Barrett, 1962;Jeanson, 1960-71). With the exception of the work of Jeanson the soils examined were organic in nature or surface horizons rich in organic matter. These soils would have developed over hundreds of years under the influence of most of the soil forming factors. Because of the lack of control over these factors it is difficult to interpret features clearly in the soil fabrics which result specifically from the activity of soil fauna. For this reason observations have been restricted to obvious features, such as faecal pellets, whose origin could be safely attributed to faunal activity. Little attention has been given to the possible role earthworms may play in developing fabric types in soil horizons dominated by inorganic components, especially with regards to plasma fabrics. The degree of control in this study permits such interpretation. The following results will demonstrate that earthworms not only influence the organic component of the soil to produce specific morphologies, but also that they can bring about changes to the fabric of soils dominated by inorganic components.

The related distribution patterns between f-members and f-matrix and their composition are described according to the terminology of Brewer and Pawluk(1975). Plasmic fabrics, pedological features and voids are described according to the terminology of Brewer(1976). A glossary of terminology used in this study is provided in Appendix X. Micromorphological descriptions of the controls and zones within the worm worked soils are given in Tables 6-9. Fabrics of the controls are shown in Plate 2 and schematic diagrams showing the location of the zones in the worm worked soils are presented as overlays on photographs of the thin sections in Plates 3,5 and 7. Micrographs showing selected features and plasma fabrics are illustrated in Plates 4,6,8-10.

4.2.1.2 Variations According to Species

Earthworms, acting alone, have the capability of forming a granular type of structure but this varies depending on the species of earthworm and texture of soil under consideration. The discussion in this section will concentrate only on changes to soil fabrics resulting from the activities of the earthworms. Fabric types resulting from the interaction of species and soil texture will be discussed in a subsequent section on variations according to soil texture(Section 4.2.1.6).

Where grass alone was added to the soil columns(Treatment 1) minor differences in the soil fabrics relative to the controls(Treatment 5) were

Table 6: Micromorphological description of fabric types in the controls for all three soil textures (Treatments 1,5).

Soil	Zone	Level of Organization	Description and Remarks
(1)' Spruce Grove	None	F-member/F-matrix	matriplectic/matrichlamydic: The fabric is dominantly matrichlamydic with very minor zones of separated plectic-porphyric fabric.
(5)Spruce Grove	None	F-member/F-matrix	orthogranic-matrichlamydic: The fabric is dominantly matrichlamydic with a minor component of orthogranic fabric and very minor inclusions of separated plectic fabric. Small packing voids are also evident.
(1)Cooking Lake	None	F-member/F-matrix	matrifragmic/metafragmoidic: The fabric is dominanted by accomodated metafragmoidic units and has an upper zone of phytogranic units. Interconnecting irregular orthovughs of variable size occur throughout the fabric. Few argillans occur as pedological features while $CaCO_3$ crystallaria are common.
		plasma	skel-vo-ma-mosepic: Skelsepic and vosepic fabrics occur as inclusions and are weakly expressed.
(5)Cooking Lake	None	F-member/F-matrix	metafragmoidic/metafragmoidic vughy porphyric: The fabric is dominantly a metafragmoidic vughy porphyric intergrade where irregular orthovughs and metavughs are small and occur frequently. The zone of vughy porphyric fabric is small. Some interconnecting metavughs are associated with the metafragmoidic fabric, while a few craze planes occur in the upper portion of the section. $CaCO_3$ nodules and crystallaria are common pedological feaatures occurring throughout the fabric while argillans are few.
		plasma	skel-vo-ma-mosepic: The plasma is complex including zones of extreme masepic and omnisepic fabrics.

Soil	Zone	Level of Organization	Description and Remarks
(1) Ellerslie	None	F-member/F-matrix	matrifragmoidic//vughy porphyric: The fabric is dominantly vughy porphyric where small irregular metavughs and small channels occur as pedological features. Much of the silt and sand occurs as calcite nodules. The matrifragmoidic fabric occurs close to the surface.
		plasma	mo-insepic: The mo-insepic fabric dominates while zones of lattisepic fabric occur as inclusions
(5)Ellerslie	None	F-member/F-matrix	vughy porphyric: The fabric is dominantly porphyric where small irregular metavughs occur frequently. Irregular bifurcated channels, horizontal craze planes, and interconnecting metavughs occur less frequently. Calcite nodules occur frequently as pedological features.
		plasma	in-mosepic

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[1]( ) indicates treatment number

COLOURED PICTURES
Images en couleur

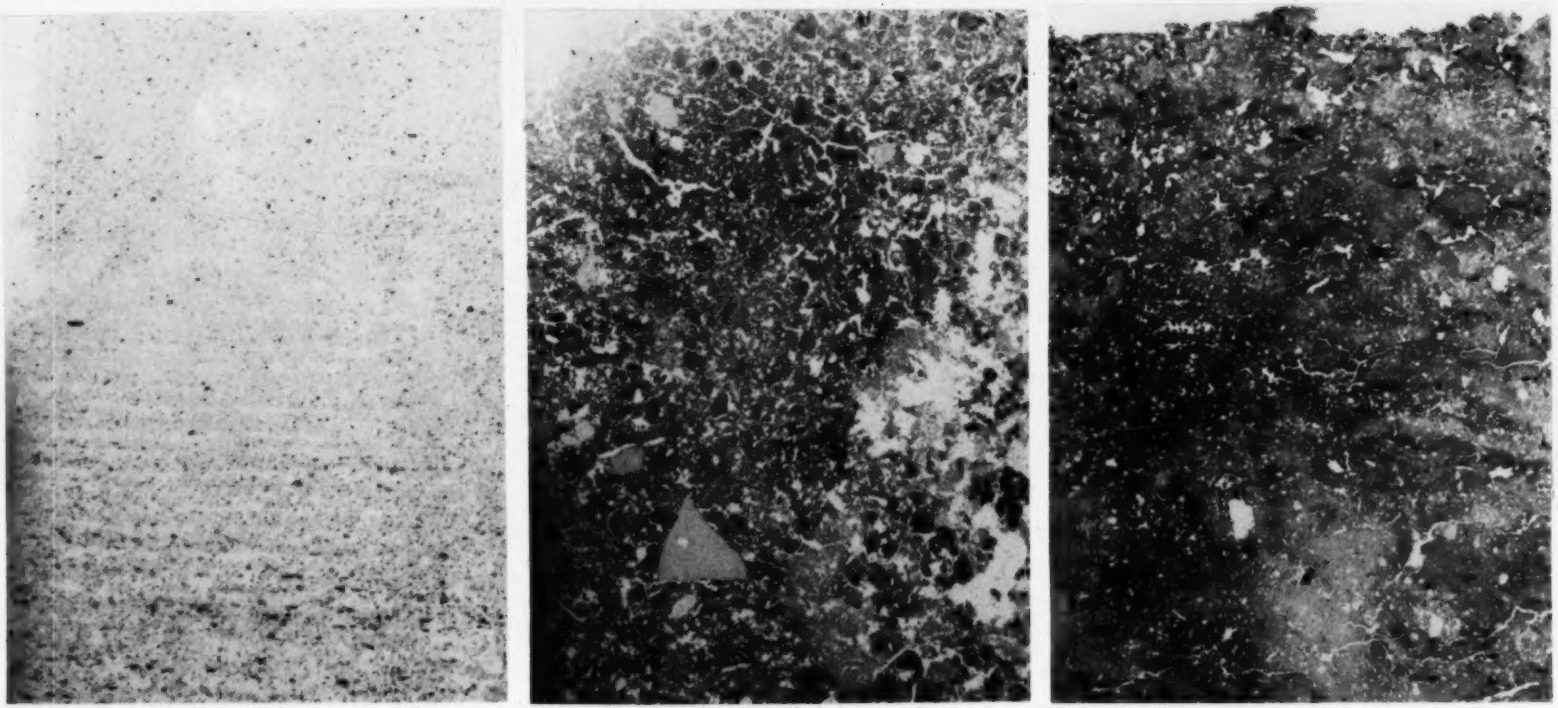

Plate 2a:Spruce Grove(sandy loam)
orthogranic-matrichlamydic

Plate 2b:Cooking Lake(clay loam)
metafragmoidic/
metafragmoidic vughy porphyric

Plate 2c:Ellerslie(silty clay loam)
vughy porphyric

Plate 2:Related distribution patterns of the F-members/F-matrix in the controls(Treatment 5).Plain light.Frame width 15mm.

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see Table 6 for descriptions

observed(Table 6;Plate 2). These differences are considered to be inconsequential in terms of reflecting alterations brought on by the presence of grass on the soil surface. They most likely result from the natural variability expected when sampling parent materials in the field. Since it is concluded that the addition of grass alone does not produce any profound alterations to the soil fabrics in this study, changes to the fabric of soils where both grass and earthworms were added can be safely attributed to the activities of the latter.

Changes to soil fabrics are different when affected by each of the ecological groups alone or when they occur together. In all treatments where earthworms were active the fabrics could be differentiated into distinct zones. These zones reflect regions in the soil where the earthworms were more, or less, active. Some generalizations can be made regarding alterations to soil fabrics resulting from the activities of similar groupings of earthworms across all three textures of soil.

Octolasion tyrtaeum and *Aporrectodea turgida* (Treatment 2)

The soils in which the epigeous species were active are characterized by the presence of two distinct zones(Plate 3;Table 7). Zone I occurs at the soil surface and is generally described as having a porphyric fabric or a mixed complex fabric of which one of the components is a porphyric fabric. The matrix material is browner in color than the underlying material in Zone II. Channels occur as pedological features along with more metavughs and fewer aggrotubules than in Zone II. The dominant fabric type of Zone II, which underlies Zone I, is similar in nature to that of the corresponding control with the exception that it typically contains inclusions of the fabric type found in Zone I. Aggrotubules and metavughs occur as pedological features and zones of compaction occur in association with some of them. Phytogranic units are absent from both zones and faecal pellets are scarce.

Zone I constitutes the region where the epigeous species were most active since its fabric is modified to a greater extent than the fabric of Zone II, relative to the controls. These species play a minimal role in mixing litter deposited on the surface into the mineral soil. This is supported

Table 7:Micromorphological description of fabric types in Treatment 2(*O. tyrtaeum*,*A. turgida*)

Soil	Zone	Level of Organization	Description and Remarks
Spruce Grove	I	F-member/F-matrix	matriplectic porphyric: Channels occur as the dominant pedological feature
	II		matriplectic: The fabric is dominated by matriplectic fabric with minor inclusions of matrichlamydic material. Both irregular orthovughs and smooth metavughs occur as pedological features.
			Both zones contain very minor inclusions or organic plasma
Cooking Lake	I	F-member/F-matrix	metafragmoidic: The fabric is dominantly metafragmoidic but includes zones of matrigranic fabric. Where fragmoidic units occur they are small. Channels, large and small smooth metavughs, as well as a few irregular metavughs are found throughout the zone. CaCO, nodules and melanons occur as pedological features. Very few faecal pellets are found at the surface.
		plasma	skel-in-masepic: Inclusions of brown plasma are evident.
	II	F-member/F-matrix	metafragmoidic porphyric: The fabric is dominantly porphyric with very minor metafragmoidic and matrigranic components. Aggrotubules, smoothed metavughs, and irregular metavughs commonly occur throughout the zone. CaCO, nodules, melanons and the rare argillan occur as pedological features.
		plasma	skel-in-masepic.
			Plasma fabrics appear denser around the channels in both zones.

Soil	Zone	Level of Organization	Description and Remarks
Ellerslie	I	F-member/F-matrix	metafragmoidic porphyric: The dominantly porphyric fabric occurs near the surface. Large smooth metavughs, and some faecal material occurs as pedological features. Small arched channels occur frequently.
		plasma	in-mosepic: The fabric includes zones of bi-masepic and concentrations of brown plasma are evident.
	II	F-member/F-matrix	vughy porphyric: The vughy porphyric fabric has numerous very small metavughs and some arched channels. Large smooth metavughs similar to those found in Zone I occur here but less frequently. Zones of compaction are evident.
		plasma	in-mosepic

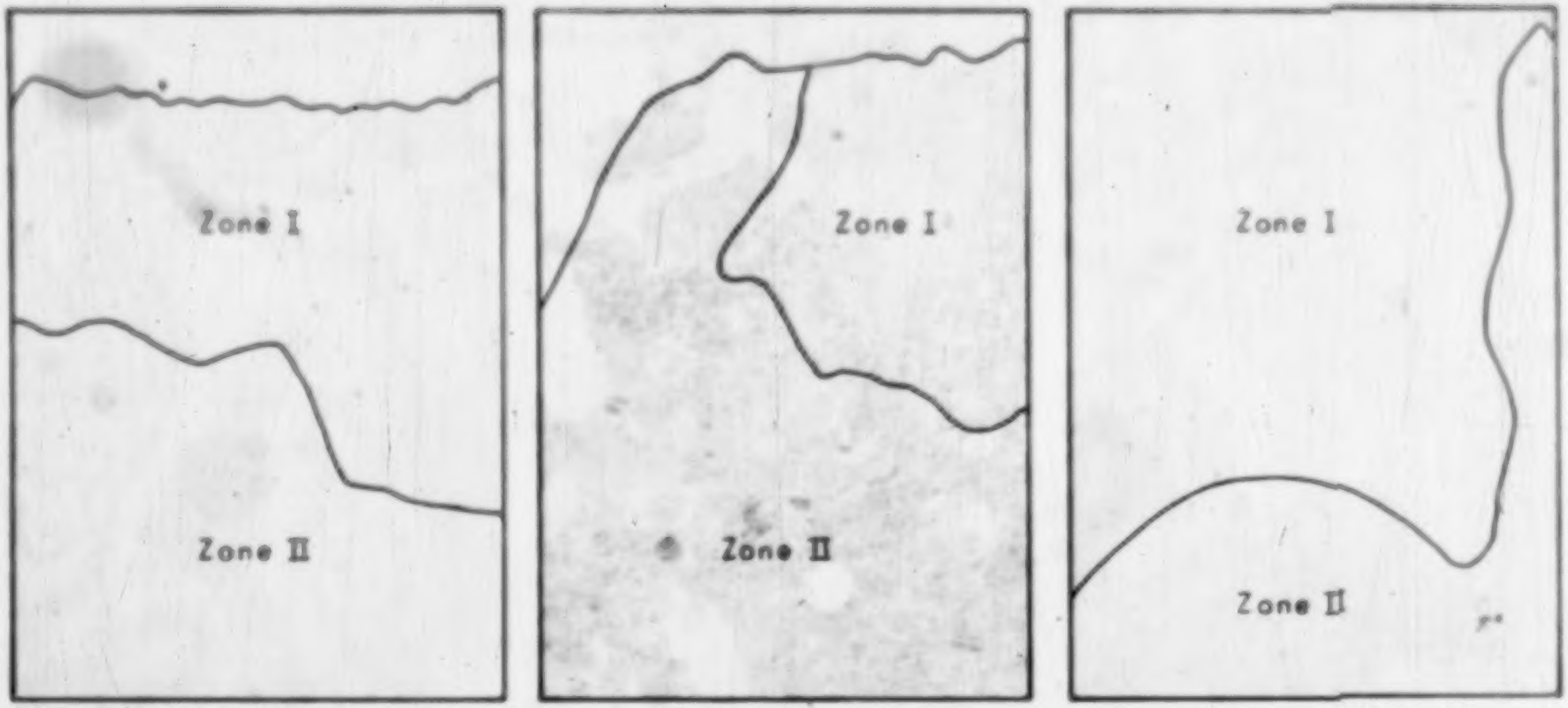
Zone I
Zone II
Zone I
Zone II
Zone I
Zone II

Plate 3a [illegible]
Zone I [illegible]
Zone II [illegible]

[illegible]

Plate 3 Relative distribution patterns of the [illegible] resulting from the activities of [illegible]

(See Table [illegible])

by the absence of phytogranic units in the soil matrix and the presence of a layer of relatively undecomposed grass which has accumulated on the soil surface in a zone distinctly separate from the mineral soil. The brownish color and increase in the concentration of plasma in Zone I shows these earthworms play an important role in the process of humification. The dominant fabric in the control for the Spruce Grove soil is matrichlamydic(Plate 7b;Table 7). Skeletal grains are randomly oriented leaving large voids. Plasma concentrations around and between the skeletal grains are minimal. The high birefringence of the plasma indicates it is dominated by clays. In Zone I of Treatment II(Plate 4a) the fabric is described as matrichlamydic-porphyric(mixed complex) where skeletal grains have been compressed together after passage through the gut of the earthworm. The voids are filled in with plasma consisting of a combination of clays and humified organic matter as indicated by the lower birefringence than that observed for the control. Changes to soil fabrics in Zone I(Treatment 2) of the Cooking Lake and Ellerslie soils are similar to those described for Spruce Grove.

These species of earthworms do not deposit faecal material on the soil surface but rather defecate in the soil while tunnelling. This is evaluated from the presence of aggrotubules and the absence of faecal

Plate 4:Fabric types resulting from activities of *L. terrestris*(Treatment 3) and *O. tyrtaeum* and *A. tugida*(Treatment 2) in the Spruce Grove soil(sandy loam).Crossed polarizers.80X.

Plate 4a:Treatment 2.Zone I.Plate 3a.

matriplectic porphyric

Plate 4b:Treatment 3.Zone I.Plate 5a.
After treatment with H_2O_2
matriplectic//matriplectic porphyric
(prior to H_2O_2 treatment)

Plate 4c:Treatment 2.Zone II.Plate 3a.
matriplectic

Plate 4d:Treatment 3.Zone II.Plate 5a.
matriplectic matrichlamydic

Legend

s)skeletal grains
v)voids
h)humified plasma
ho)humified plasma removed
after H_2O_2 treatment

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see Table 7:descriptions for Treatment 2
Table 8:descriptions for Treatment 3

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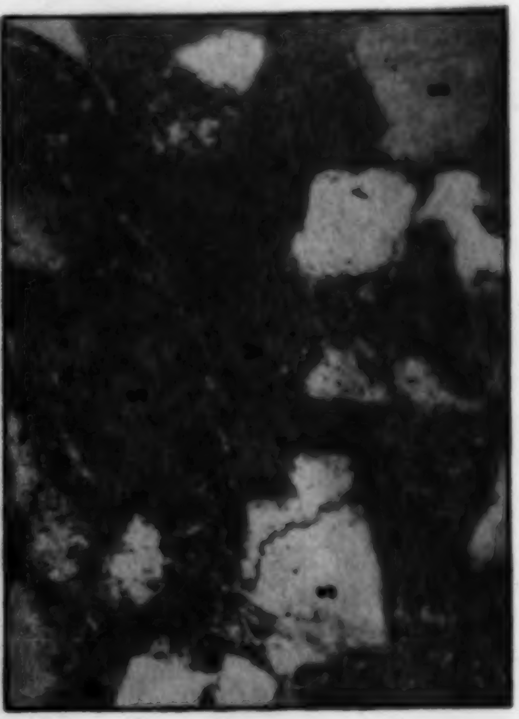

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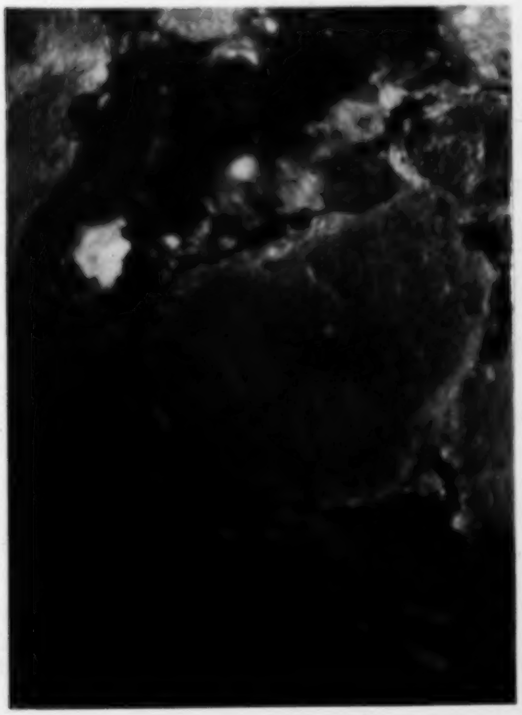

material deposited on the surface is evidence for this. While tunnelling the earthworm ingests matrix material which undergoes humification and plasmification during passage through the gut. Bal(1982) suggested that humification in the excrement of earthworms results, in part, from autooxidation of low molecular weight nitrogenous compounds in an aklaline environment created by the presence of NH_3 secreted in the gut. Contributions to humification through the influence of earthworms on microbial populations is also significant but will be discussed in a latter portion of this thesis. The modified soil material is excreted as a plastic, fluid-like mass which easily conforms to the shape of the tunnel behind the earthworm and fills it in. This behaviour of infilling tunnels forces the earthworm to construct new tunnels and by doing so the earthworm continually ingests matrix material including that which has already been modified. This further intensifies the processes of humification, plasmification and compression of the matrix material resulting in the shift towards fabrics different from the previously existing matrichlamydic, matrifragmoidic or vughy porphyric fabrics observed in the controls.

Profound alterations to soil fabrics resulting from the activities of these earthworms are largely restricted to the upper region of the soil(Zone I).

This most likely reflects their feeding habit. These earthworms do not ingest raw organic matter(i.e. litter) but rather finely divided organic matter or microorganisms existing in the soil matrix. In this experiment food of this type probably occurred in association with the litter layer. Consequently earthworms were most active in the the zone immediately underlying the grass. The feeding habit of these earthworms requires ingestion of large quantities of soil in order to receive adequate nutriment. Therefore large volumes of soil are subject to ingestion and reingestion further contributing to processes that develop a modified fabric and result in homogenization of the soil.

Zone II is characterized by mixed complex fabrics which are similar to those of the corresponding controls, but have inclusion of material modified in Zone I and transported in by the earthworms. The micrograph in Plate 4c provides a closer view of the mixed fabric in Zone II(Treatment 2) of the Spruce Grove soil. Compressed skeletal grains and voids infilled with plasma concentrations(A) occur in close proximity to randomly oriented skeletal grains where voids remain empty(B). If the experiment had continued for a longer period of time the transport of material from Zone I into Zone II would probably be much greater. In a natural system where the occurrence of microorganisms is more widespread than in the soil columns and rooting systems are present it is likely that the effect of these earthworms on soil fabrics would be less restricted due to the availability of these food sources. Jeanson(1971) found in microcosm studies that the zone of greatest activity for the species *Allolobophora ictera* was largely determined by the placement of the substrate within the soil.

The type of voids formed by these species are dominantly channels and large smooth metavughs formed by tunnelling, as opposed to mammilate or interconnecting vughs which result from the deposition of casts on the soil surface. The contribution of these voids to total pore volume may be minimal since it appears they are formed at the expense of smaller voids such as the irregular ortho- and metavughs, packing voids, channels and craze planes observed in the control soil fabrics. Although numerous channels occur throughout the soil volume they are discontinuous and may not contribute significantly to the drainage of free water. When the columns of Treatment 2 were leached water was observed to become entrapped in the channels. The channels created by these species may be important to water retention since the matrix material surrounding them is compacted and colloidal in nature and contains in smaller sized pores.

Tunnels created by *A. turgida* and *O. tyrtaeum* may be most important to soils which are compacted or have a high bulk density. Dexter(1978) demonstrated the ability of *Allolobophora caliginosa* to eat its way through high bulk density soils. *Aporrectodea turgida* and *O. tyrtaeum* also have the ability to construct channels by ingesting soil material as opposed to some other species which must force or push their way through the soil. These earthworms when introduced to the soil columns immediately tunnelled into and throughout the entire soil volume. Conversely when specimens of *L. terrestris* were introduced to the columns they could not penetrate the soil cores at the column surface. The author had to assist their entry into the soil by making a small hole in the core. The bulk density of the cores used were 1.75 g/cm^3(Spruce Grove) and 1.52 g/cm^3 and and 1.47g/cm^3 for Cooking Lake and Ellerslie soils respectively.

The foregoing discussion on the effects of *Aporrectodea turgida* and *O. tyrtaeum* on soil fabrics strongly parallels the observations of Bal(1982) regarding the species *Allolobophora chlorotica* and *A. rosea*. He referred to these species as geophages and it is proposed here that the species of *O. tyrtaeum* and *Aporrectodea turgida* be considered in a like manner. Geophages play an important role in soil genesis by ingesting, modifying the fabric of, and homogenizing large quantities of soil. They have the ability to create voids and channels in highly compacted soils and most importantly conclude the series of processes leading to humification.

Lumbricus terrestris(Treatment 3)

Soil fabrics resulting from the activities of *L. terrestris* can be divided into two zones as with the epigeous species(Plates 5;Table 8). Where these zones occur and the degree to which the fabrics were altered differ from what was previously described for *O. tyrtaeum* and *A. turgida*.

In all soils Zone I occurs in association with a singular, large vertical channel and at the soil surface. The fabric is dominantly porphyric and the matrix is high in humic material. Phytogranic units are admixed in the matrix material and occur in association with faecal pellets deposited on the soil surface. Zone I is typically separated from Zone II by planar voids. Zone II occurs in all regions outside of Zone I. The fabrics are similar to those described for the corresponding controls with the exception of very minor inclusions of smoothed metavughs and faecal pellets.

Behavioral patterns of *L. terrestris* which are distinct from those of the geophages are responsible for the differences observed in the soil fabrics.

Table 8:Micromorphological description of fabric types in Treatment 3(*L. terrestris*)

Soil	Zone	Level of Organization	Description and Remarks
Spruce Grove	I	F-member/F-matrix	matriplectic//matriplectic porphyric: This fabric occurs in association with the large channels. Phytogranic units occur near the surface where they are admixed with matrix material. The matrix is high in humic material.
	II		matriplectic matrichlamydic: Faecal pellets occur in isolated areas and where they fuse, irregular ortho-joint planes form. Zone I and Zone II are separated by large ortho-joint planes.
Cooking Lake	I	F-member/F-matrix	porphyric: The dominant fabric type is porphyric with inclusions of phytogranic units and it is mainly associated with the large vertical channel. Elongated phytogranic units give the appearance of a striated fabric to this zone. Welded faecal pellets occur near the surface in association with oblique craze plane voids having a dendritic pattern. Spherical carbonate nodules with a concentric internal fabric occur as pedological features.
		plasma	in-skel-masepic: The zones of insepic and skelsepic are few and isolated. The development of unistrial masepic is strong.
	II	F-member/F-matrix	metafragmoidic//vughy porphyric: The fabric is dominantly metafragmoidic//vughy porphyric where the metafragmoidic units are partially accomodated. Small smoothed metavughs occur throughout the porphyric fabric. A long oblique craze plane with a trellis pattern separates the metafragmoidic fabric from the vughy porphyric fabric.
		plasma	skel-vo-in-masepic: complex plasma fabric: Where vosepic fabrics occur they are strongly expressed. Some zones of masepic fabrics are striated and the fabric includes isolated zones of omnisepic fabric.

Soil	Zone	Level of Organization	Description and Remarks
Ellerslie	I	F-member/F-matrix	porphyric: The dominantly porphyric fabric occurs near the surface and in a association with the large vertical channel. It is characterized by the presence of numerous interconnecting irregular smooth metavughs. Numerous faecal pellets and welded faecal pellets occur near the surface. Carbonate glaebules and nodules occur as pedological features.
		plasma	in-ma-mosepic: Striated masepic fabric occurs within faecal material. Otherwise masepic fabrics occur along the edges of faecal pellets and in tunnel linings. Concentrations of brown plasma are evident, especially within faecal pellets.
	II	F-member/F-matrix	vughy porphyric: The fabric is dominantly vughy porphyric having numerous small irregular metavughs. Few channels, numerous small arched channels, and calcitic nodules occur as pedological features.
		plasma	in-mosepic: Zones of lattisepic fabric occur as very minor inclusions.

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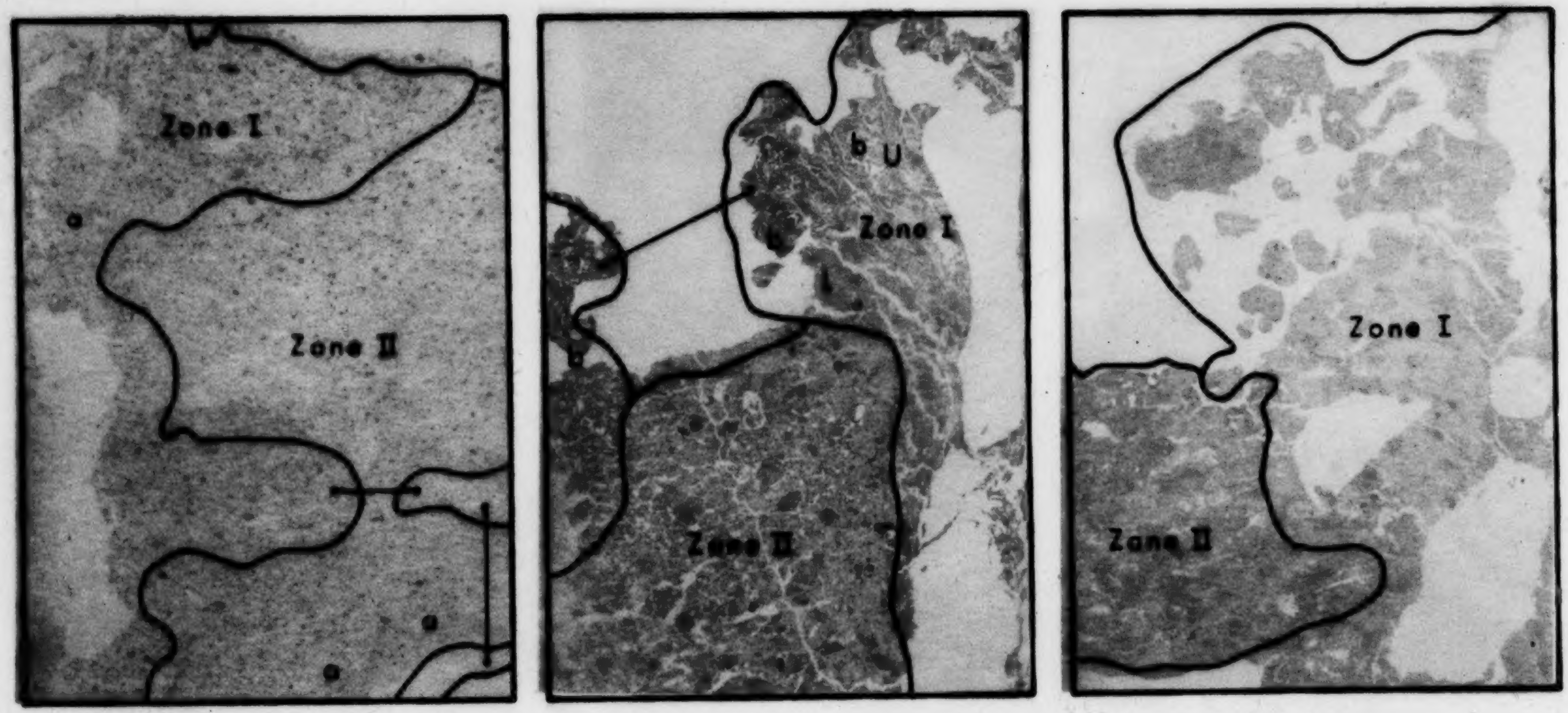

Plate 5a:Spruce Grove(sandy loam)
Zone I :matriplectic//
matriplectic
porphyric
Zone II:matriplectic
matrichlamydic

Plate 5b:Cooking Lake(clay loam)
Zone I :porphyric

Zone II:metafragmoidic//
vughy porphyric

Plate 5c:Ellerslie(silty clay loam)
Zone I :porphyric

Zone II:vughy porphyric

Legend

a)faecal deposits occurring as discrete units.
b)spherical carbonate nodules with concentric internal fabric.
U)upper zone of midden.
L)lower zone of midden.

Plate 5:Related distribution patterns of the F-members/F-matrix resulting from the activities of *L. terrestris*(Treatment 3)Plain light.Frame width 15mm.

see Table 8 for descriptions

The absence of a layer of grass accumulated at the soil surface and the admixing of phytogranic units into the matrix material(Plate 6a) indicates the importance of *L. terrestris* in withdrawing litter from the soil surface, bringing it into intimate contact with the inorganic soil components and accelerating the process of decomposition. Electron micrographs(Plates 7c,7d) clearly show the ability of *L. terrestris* to mix and bind soil organic and inorganic components. Once soil has passed through the gut of the earthworm skeletal grains are embedded in a mass of colloidal material and intermixed with organic fragments(p)(Plate 7c). In the unaltered material sand grains remain as distinct, randomly oriented units separated by large voids(Plate 7d). The degree of humification observed in Zone I is greater than that observed in the corresponding zone produced by the epigeous species. The birefringence of humified plasma formed under the influence of *L. terrestris*(Plate 7a) is much lower than that of plasma formed by the epigeous species(Plate 4a). Once treated with H_2O_2 most of the plasma in Zone I of Treatment 3 was oxidized and the brown color disappeared indicating the plasma consisted largely of organic rather than inorganic colloidal material(Plates 7a,4b;10c,10d). The dominance of humified organic matter in the plasma of Zone I(Treatment 3) most likely reflects the

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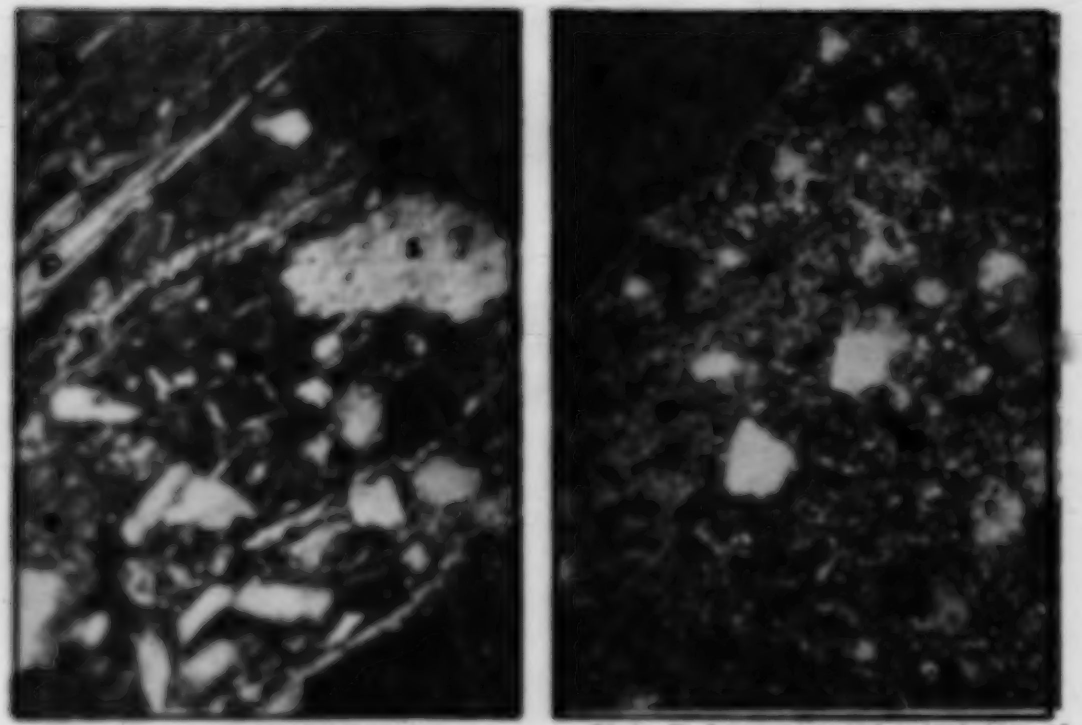

Plate 6a Admixture of elongated phytogenic units with matrix material in faecal deposits 20x.

Plate 6b Compaction and orientation of clays and organic plasma around a channel 80x.

Legend
p phytogenic units
s skeletal grains
m matrix.
v voids
o oriented clays

Plate 6 Features produced in the fabric of Treatments 3 and 4 in the Cooking Lake soil through the action of earthworms.Crossed polarizers.

Plate 7:Photomicrographs and electron micrographs of fabric types
occuring in Treatment 3 and Treatment 5 of the Spruce Grove soil.

Plate 7a:Treatment 3.Zone I.Plate 5a.crossed polarizers.80X.
matriplectic//matriplectic porphyric

Plate 7b:Treatment 5.Plate 3a.crossed polarizers.80X.
orthogranic-matrichlamydic

Plate 7c:Electron micrograph of fabric in Plate 7a.

Plate 7d:Electron micrograph of fabric in Plate 7b.

Legend
s)skeletal grains.
v)voids
h)humified plasma.
p)phytogranic units.

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see Table 6:descriptions for Treatment 5.
Table 8:descriptions for Treatment 3.

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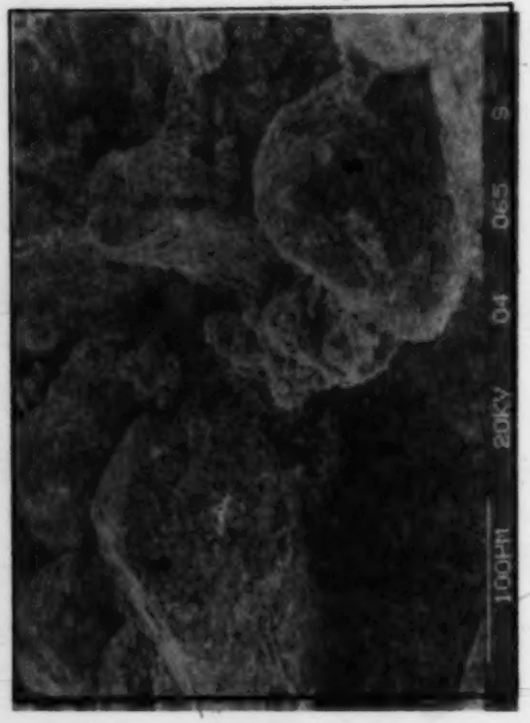
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feeding habit of *L. terrestris*. Large amounts of organic matter were ingested and then subjected to transformations leading to the formation of humic material during, or immediately after, passage through the gut. The intimate mixing of organic and inorganic components by these earthworms indicates they play a more important role than geophages in initiating the formation of a mull-type of structure. Large planar voids which separate the soil material altered by *L. terrestris* in Zone I from unaltered material in Zone II(Plate 5) suggests the existence of strong binding between soil components in Zone I.

Thus, several processes considered important to the development of a mull-type of fabric are greatly enhanced by the activities of *L. terrestris*. These include humification, intimate mixing of inorganic and organic components and strong binding of the soil matrix material. Although the changes to soil fabric effected by *L. terrestris* are more profound than those attributed to *O. tyrtaeum* and *A. turgida* they occur only on a localized basis. The clear separation between Zone I and Zone II and the strong similarity between the fabric of Zone II and the controls indicates that much of the soil volume has remained untouched by *L. terrestris*. A comparison of fabrics in Zone II of Treatment 2(Plate 4c) and of Treatment 3(Plate 4d) to that of the control(Plate 7b) shows that *L. terrestris* transported little of the material modified in Zone I into the bulk of the soil material as compared to the epigeous species. Strongly modified material occurs only as a narrow band lining the few large channels and as surficial deposits. *L. terrestris* constructed permanent tunnels and the faecal material served to line and stabilize them. Once the tunnels were stabilized faecal material was deposited on the soil surface. In some cases these deposits occur as distinct granular units(Plate 5c) but in general they are fused together allowing the earthworm to extend the length of its tunnel. These mounds formed by *L. terrestris* are commonly referred to as middens. Surficial deposits of faecal material by *L. terrestris* may contribute to the formation of granular units but only to a limited extent. Their major contribution to the development of a mull-type of structure comes through intimate mixing of organic and inorganic soil components, enhancing humification and increasing the strength of binding between soil particles.

Channels formed by these earthworms are open to the surface, permanently constructed and vertical in orientation and probably contribute greatly to the drainage of free water. The retention of water may also be enhanced by the presence of faecal material as lining in the channels since it has more colloidal and organic material in it than the surrounding matrix material(Plate 6b).

Octolasion tyrtaeum, *Aporrectodea turgida* and *Lumbricus terrestris*(Treatment 4)

In this treatment soil texture emerged as a very important factor controlling the type of fabric observed. Thus it was difficult to generalize about the interactions of the two ecological groups of earthworms. The influence of soil texture on fabric type was also observed in Treatment 3 but enough similarities in modifications existed across all three textures to permit discussion. The reader should bear in mind that the following discussion is cursory in nature since a more detailed explanation of results is provided in a subsequent section on variations in fabrics according to soil texture.

Descriptions of soil fabrics are divided into distinct zones as with the other treatments although all zones are not common to all soil textures(Plate 8;Table 9). Zone I constitutes the region where the greatest effect resulting from the interaction of the two ecological groups is observed. No grass has accumulated on the soil surface reflecting its admixing into the matrix material by *L. terrestris*. Once the grass was drawn down into the matrix material it became available for ingestion by the epigeous species as well as *L. terrestis*. Therefore

Table 9:Micromorphological descriptions of fabric types in Treatment 4(*L. terrestris*,*O. tyrtaeum*,*A. turgida*)

Soil	Zone	Level of Organization	Description and Remarks
Spruce Grove	I	F-member/F-matrix	metafragmoidic matrichlamydic-matriplectic: The fabric is dominantly composed of faecal material which is fused to form irregular joint planes.
	II		metafragmoidic porphyric-matriplectic: The porphyric-matriplectic fabric occurs as channel linings while the faecal units along with some phytogranic units occur near the surface of the large channel.
	III		porphyric/matriplectic/matrichlamydic: Isolated separated zones of matrix material form the porphyric component. Otherwise the fabric is dominantly matrichlamydic with a minor matriplectic component. Some faecal pellets and numerous small irregular orthovughs occur as pedological features.
Cooking Lake	I	F-member/F-matrix	metafragmoidic porphyric: The fabric is dominantly metafragmoidic porphyric with inclusions of phytogranic units. The fabric is formed from welded faecal material which is perforated by large smooth metavughs. Few carbonate nodules and crystallaria occur as pedological features.
		plasma	in-masepic: The masepic fabric is strongly developed and striated. Brown plasma concentrations occur in the faecal deposits.
	III	f-member/F-matrix	matrifragmoidic porphyric/vughy porphyric: The fabric is dominantly matrifragmoidic porphyric with phytogranic units occurring in isolated areas. Aggrotubules, smoothed metavughs, carbonate crystallaria, and craze planes occur throughout the zone as pedological features.
		plasma	omni-masepic: Masepic fabric dominates the entire zone while areas of omnisepic fabric occur as inclusions.

Soil	Zone	Level of Organization	Description and Remarks
Ellerslie	I	F-member/F-matrix	phyto-matrigranic: This zone occurs on the surface and is comprised of large phyto-matrigránic units. These units are formed from faecal pellets and welded faecal pellets which have been deposited on the surface.
		plasma	in-mosepic: Humic plasma concentrations are centrally located within faecal pellets along with insepic plasma. The mosepic fabric occurs around the edges of faecal pellets.
	II	F-member/F-matrix	metafragmoidic porphyric: The dominantly porphyric fabric which occurs at the surface is characterized by the presence of numerous small channels which are randomly oriented. Carbonate glaebules occur as pedological features.
		plasma	mo-masepic: Brown plasma concentrations occur throughout the zone.
	III	F-member/F-matrix	porphyric: This porphyric fabric is characterized by the presence of few craze planes. Large smooth metavughs and some aggrotubules occur as pedological features
		plasma	mo-in-masepic: The dominant fabric is masepic. Mosepic and insepic fabrics occur in separated zones. Plasma concentrations are higher and slightly humified around the channels.

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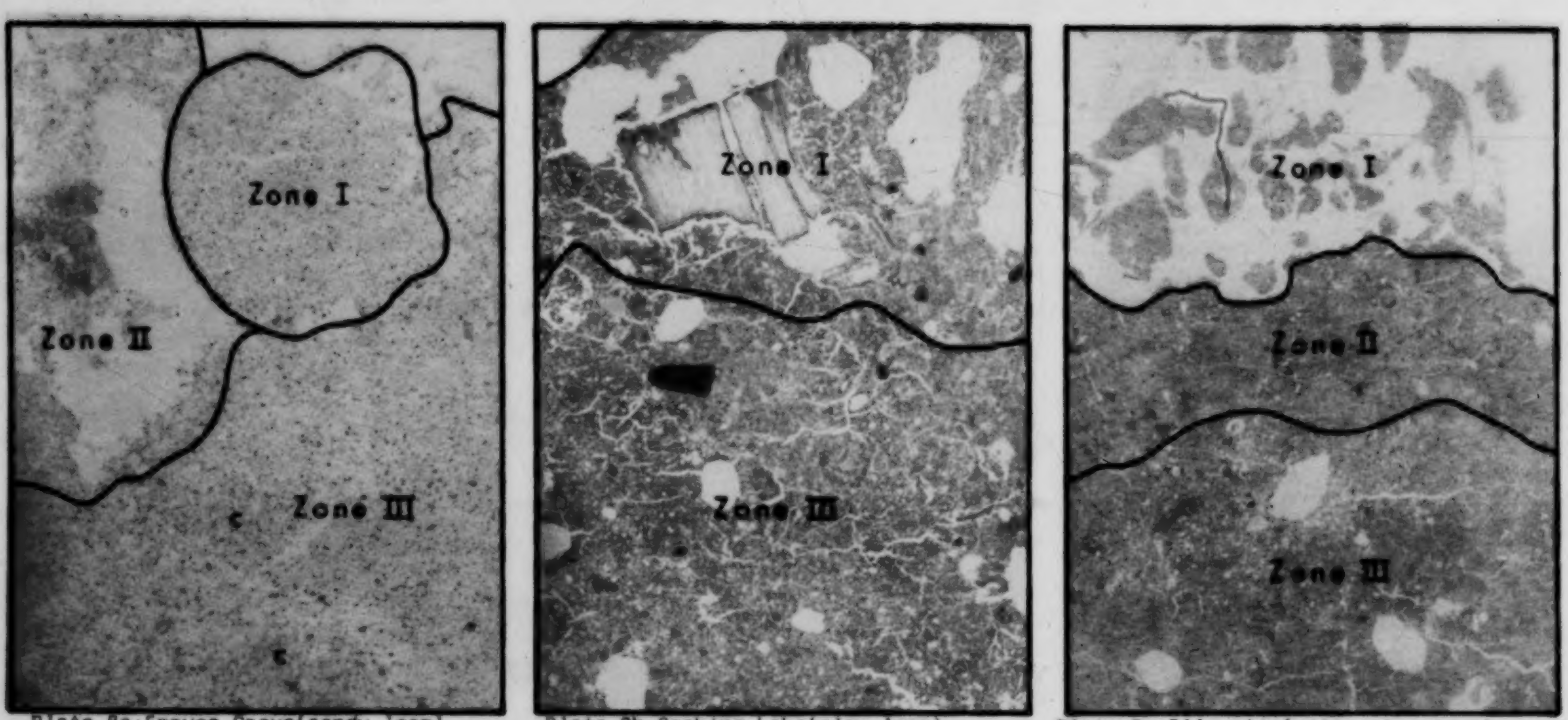

Plate 8a:Spruce Grove(sandy loam)
Zone I :metafragmoidic
matrichlamydic
matriplectic
Zone II :porphyric-matriplectic

Zone III:porphyric/
matriplectic/
matrichlamydic

Plate 8b:Cooking Lake(clay loam)
Zone I :porphyric

Zone III:matrifragmoidic
porphyric/
vughy porphyric

Legend
c)faecal pellets occurring as discrete units.

Plate 8c:Ellerslie(silty clay loam)
Zone I :phyto-matrigranic

Zone II :metafragmoidic
porphyric
Zone III:porphyric

Plate 8:Related distribution patterns of the F-members/F-matrix resulting from the activities of *O. tyrtaeum*, *A. turgida* and *L. terrestris*(Treatment 4).Plain light.Frame width 15 mm.

see Table 9 for descriptions.

less large and more small phytogranic units are present in Zone I in these soils than in Zone I of Treatment 3. Middens resulting from the activity of *L. terrestris* are no longer present since this soil material has been ingested and redistributed on the soil surface by *O. tyrtaeum* and *A. turgida*. The combined activity of the two ecological groups has led to the development of a region(Zone I) at the soil surface characterized by the presence of many individual faecal pellets and/or fused faecal pellets. The matrix material is humified in most cases since the organic component was subjected to transformation by both groups of earthworms.

Zone III is common to all three textures of soil and occurs in the lower most portion of the section. It is characterized by mixed or separated complex fabrics, and the presence of smoothed metavughs, few phytogranic units, aggrotubules and faecal pellets. The fabrics occurring in this zone roughly correspond to those of Zone II in Treatment 2. The major difference lies in the fact that the porphyric component of the fabrics increases in dominance and phytogranic units are present. The epigeous species have translocated material modified by *L. terrestris*, which occurs only in isolated regions in Treatment 3(Zone I), into the bulk of the matrix material. The net result is a mixed or separated complex fabric characterized by zones of porphyric fabric. The appearance of phytogranic units in Zone III suggests that once *L. terrestris* has initially drawn the grass into the soil matrix the epigeous species transport this material to a lower depth thus further enhancing the contact between the inorganic and organic soil components.

The presence of both ecological groups of earthworms had a synergistic effect in terms of development of soil fabrics. *L. terrestris* played a dominant role in initiating the mixing of inorganic and organic constituents and enhancing humification and binding between soil components. *O. tyrtaeum* and *A. turgida* further enhanced humification by ingesting litter admixed with the soil matrix by *L. terrestris* as well as faecal deposits of *L. terrestris*. More importantly they homogenized the soil fabric by transporting organic and inorganic components mixed and modified by *L. terrestris* into the bulk of the soil volume.

Additional zones of unique fabrics were observed in some of the soils from this treatment(Zone II - Fig. 6c,8c). These fabric characteristics along with other unique characteristics in Zones I and III reflect differences in soil texture and their interaction with species. These differences will be discussed in more detail in the following section.

4.2.1.6 Variations According to Texture

The previous discussion focussed on differences in soil fabrics that reflect the activities of different groupings of earthworms. Although the following discussion is sub-divided in a similar fashion(according to species) the emphasis will be on the fabrics observed as a result of species interaction with soil texture.

Differences in fabric types resulting from species-texture interaction are particularly evident in soils where *L. terrestris* was active either alone(Treatment 3) or in association with the epigeous species(Treatment 4). Only minor differences in fabrics resulting from the interaction between species and soil texture were observed in soils where epigeous species were active alone(Treatment 2).

Octolasion tyrtaeum and *Aporrectodea turgida* (Treatment 2)

The fabric descriptions for the sandy loam soil(Spruce Grove) in which *O. tyrtaeum* and *A. turgida* were active provide little evidence to indicate that a granular type of structure is developing. No faecal pellets or aggrotubules occur as discrete units and no granoidic or fragmoidic fabrics are present(Table 7;Plate 3a). The presence of a matriplectic porphyric fabric in Zone I indicates these earthworms have some influence in binding soil components together. In the absence of a significant clay component the strength of binding is not great enough to result in the formation of discrete faecal pellets leading to the development of a granular type of structure. It is probable that the majority of soil occurring in Zone I has passed through the gut of the earthworm and as such constitutes faecal material which has fused together forming a porphyric intergrade fabric. Skeletal grains were pressed together either by passing through the gut of the earthworm or as a result of tunnelling. Organic plasma formed through the action of these earthworms acts as a cementing agent which binds the skeletal grains together(Plate 4a). Because a significant clay component is not present one could speculate that the organic plasma is not stabilized or protected against further degradation. Therefore the binding effect is expected to be temporal in nature. In a natural system where sandy textured soil exists the activities of these earthworms may result in a net benefit in terms of soil stabilization. At least some agent is present which can enhance binding and stabilization of the soil even if it is temporal. If significant populations of these earthworms are present one would expect binding of soil components under their influence to be a continuous process compensating for degradation of previously formed plasma.

Where the clay content of the soil is higher(Cooking Lake and Ellerslie soils) than in the Spruce Grove soil discrete granular units were formed. They only occur infrequently(Plates 3b,3c). Although the clay content of the Ellerslie and Cooking Lake soils is similar (Table 5) alterations to soil fabrics as a result of the activities of epigeous species are different.

The formation of granular units is most noticeable in the Cooking Lake soil where a small area of matrigranic fabric occurs in Zone I and metafragmoidic units are much smaller than those observed in the control. Faecal pellets and aggrotubules occurring as discrete units are more common than in the Ellerslie soil. In the Ellerslie soil faecal pellets rarely occur, no aggrotubules are present and the fabric is porphyric in both Zones I and II.

Changes to plasmic fabrics in the Ellerslie soil are minimal. In-mosepic fabrics dominate both Zones I and II of Treatment 2 as well as the controls(Treatments 1,5;Tables 6,7). Zone I is slightly modified as indicated by the appearance of zones of bimasepic fabric and brown plasma concentrations. As with observations at the F-fabric level of organization the most significant changes to plasmic fabrics occurred in the Cooking Lake soil. Skel-vo-ma-mosepic fabrics dominate the controls(Table 6;Plate 9a) while skel-in-masepic fabrics dominate both zones of the soil in Treatment 2(Table 7). Zones of strongly oriented clay are commonly observed throughout the matrix material(Plate 9b) and around channels and smooth metavughs.

The foregoing observations indicate that these earthworms have the ability to alter both plasma fabric types and related distribution patterns at the F-fabric level of organization. Brewer(1976) stated that plasma fabrics of the type observed in the worm-worked soils are related to stresses such as wetting and drying or shrinking and swelling. Most likely similar stresses are involved in producing the changes to plasma fabrics observed in this study where the earthworms act as the agents who physically move the matrix material or modify it so that it is subject to change through physical forces. In the case of the Cooking Lake soil the vosepic component is lost and an insepic component appears. This may result from tunnelling activities which compress the matrix material together so that voids are lost and previously existing cutans are forced together increasing the dominance of the insepic and masepic components. Zones of oriented clays commonly observed in the Cooking Lake

Plate 9:Micrographs of plasma fabrics occurring in Treatments 2,4, and 5
in the Cooking Lake soil.Crossed polarizers.80X.

Plate 9a:Treatment 5.Plate 2b.

Plate 9b:Treatment 2.Zone I.Plate 3b.

Plate 9c:Treatment 4.Zone I.Plate 8b.
in-masepic(unistrial)

Plate 9d:Treatment 4.Zone I.Plate 8b.
humified plasma in faecal deposits

Legend
s)skeletal grains.
v)voids.
m)matrix.
h)humified plasma.
o)oriented clays.

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see Table 6:descriptions for Treatment 5
Table 7:descriptions for Treatment 2
Table 9:descriptions for Treatment 4

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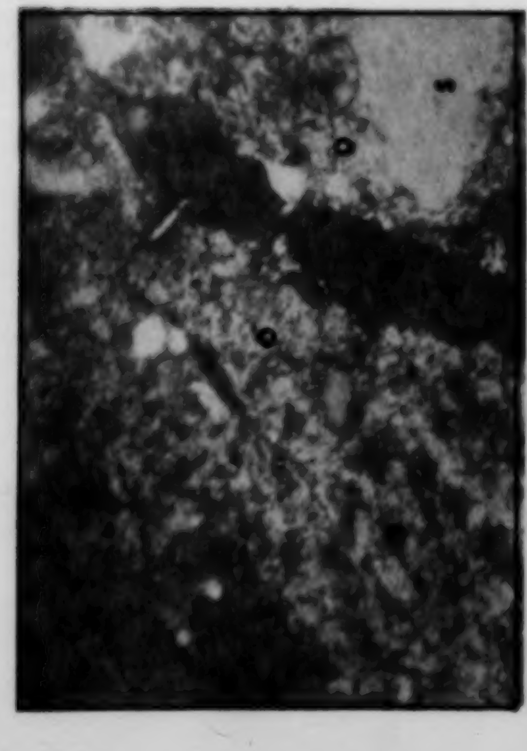

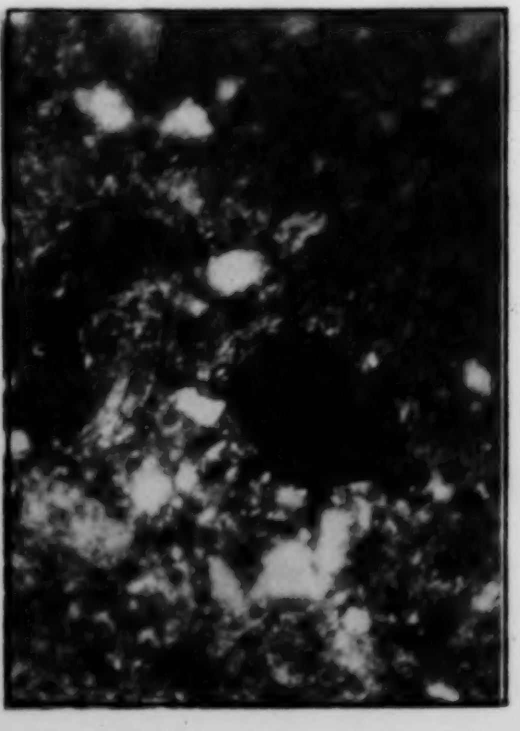

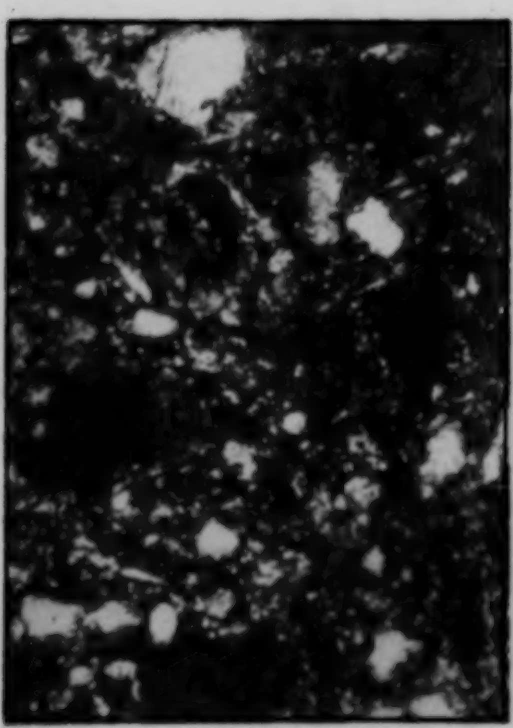

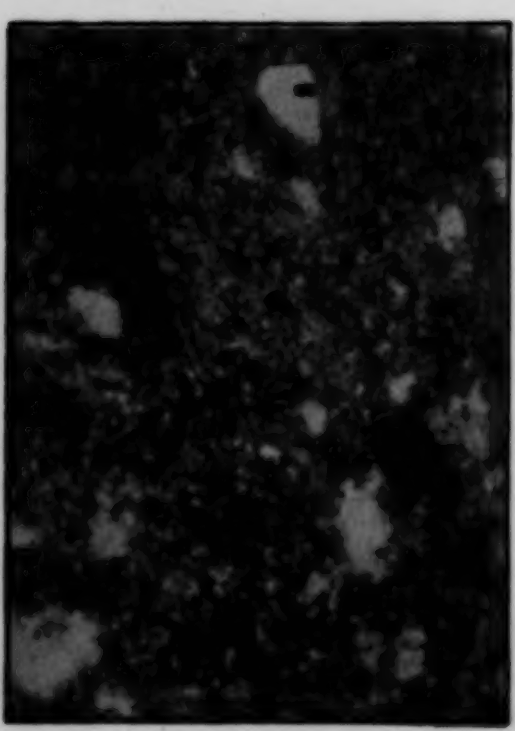

soil(Plate 9b) may result from physical alterations to the matrix material while passing through the gut of the earthworm. When soil material passes through the gut of an earthworm and during egestion it is in a semi-fluid state(Guild,1955). The matrix material is subjected to physical forces such as increased pressure and compression during passage through the gut. Together the pharynx and gizzard of the earthworm act as a pump which aids the peristaltic action of the gut in forcing ingesta along the food tract. A series of valves along the tract control the direction and speed of flow(Arthur,1965). Soil in a semi-liquid state subjected to these forces may be reorganized and orientation of the clay domains may increase.

Why alterations to both plasma and F-fabrics are greater in the Cooking Lake soil than in the Ellerslie soil is not clear. Because clay contents of both soils are similar these differences can not be attributed to the quantity of clay available for ingestion, subjection to physical forces or involvement in complexing with organic matter. Differences in fabric types may, in fact, reflect the relative proportions of silt and sand. Mucopolysaccharides excreted from mucin ducts in the pharynx region of *Lumbricus sp.* and *Allolobophora sp.* serve to lubricate the passage of ingesta through the food tract(Arthur,1965). The presence of a greater amount of sand in the Cooking Lake soil(35% versus 8.6% for the Ellerslie soil) may aggravate the intestine such that it increases the secretion from the mucin ducts. Mucopolysaccharides have been implicated in enhancing binding(Theng,1979) and this may account for the observed increase in aggrotubules and faecal pellets occurring as discrete units in the Cooking Lake soil. It may also account for the high concentrations of organic plasma observed in the Spruce Grove soil where earthworms were active(Plate 4a). Alternatively the presence of discrete units in the Cooking Lake soil may be due to the higher amount of organic carbon inherent in it(1.24% as opposed to .54% in the Ellerslie soil).This value indicates more organic matter may be available in the matrix material of the Cooking Lake soil for binding with inorganic components after ingestion by the epigeous species. The value for organic carbon may be erroneously high as an indicator of soil organic matter since carbon from coal present in the Cooking Lake soil would be included in the organic carbon determination.

The higher frequency in occurrence of oriented clays observed in the Cooking Lake soil may also have resulted from preferential ingestion of small sized particles in the soil. Piearce(1978) determined the maximum length and width of mineral particles in the gut of *Allolobophora chorotica*(a geophage) to be .58 mm. and .41 mm. respectively. This falls into the fine to medium sand size range of particles according to the Canadian system of classification. In the Cooking Lake soil where larger particle sizes occur more frequently than in the Ellerslie soil the earthworm may avoid them and preferentially ingest the smaller sized particles. These would then be subjected to stresses leading to increased orientation of the clay domains. In the Ellerslie soil particles falling in the sand size range occur less frequently and therefore little preferential ingestion would occur.

Lumbricus terrestris(Treatment 3)

As previously stated in Section 4.2.1.2 the influence of *Lumbricus terrestris* on soil fabrics is far more profound than those resulting from the epigeous species. The effect of this species on fabric type also varies significantly depending on the soil texture(Plate 5;Table 8).

Guild(1955) stated that when earthworms are active in light textured soils less faecal material is excreted at the soil surface since it is used to line and stabilize tunnels. Conversely in clay soils more material is ingested and expelled on the surface since less is required to stabilize the tunnels. This conclusion is consistent with observations in this study. In the Spruce Grove soil(Plate 5a) little faecal material is deposited on the soil surface and few granular units are present. Conversely in the Cooking Lake and Ellerslie soils(Plates 5b,5c) more faecal material is deposited on the soil surface and in the Ellerslie soil it occurs more frequently as discrete faecal units.

The formation of brown plasma concentrations by *L. terrestris* is greater than that formed by the epigeous species(Plates 4a,7a). This, in part, probably reflects the feeding habit of *L. terrestris* as mentioned in section 4.2.1.2. The intensity in development of brown plasma concentrations within Treatment 3 is greatest in the faecal material occurring in the Spruce Grove and Cooking Lake soils(Zone I in Plates 5a,5b;micrographs in Plates 7a,9d). This plasma development may reflect contributions from both mucoid secretions which are increased due to the aggravating presence of a high proportion of sand and decomposing organic matter from litter ingested by the earthworms. Contributions to organic plasma from both these sources appear to have a more positive affect on structural development in the sandy soil(Spruce

Grove) compared to the clay loam soil(Cooking Lake). In the absence of a significant clay component(Spruce Grove) organic plasma formed by *L. terrestris* led to the formation of some faecal deposits occurring as discrete units in the main tunnel area and around channels(Plate 5a-(a)). Piearce(1981) concluded that body secretions of earthworms played an important role in binding sand into water stable aggregates. In the Cooking Lake soil organic plasma occurs in intimate association with oriented clays(unistrial fabrics) leading to fusion of the faecal material(midden-Plate 5b). Agarwal et al.(1958) attributed the fusion of soil with a clay loam texture and under the influence of earthworms to excretion of "some colourless waxy fluid from their nymphridia".

In the Ellerslie soil less sand is present to induce mucoid secretion and the development of brown plasma is not as great as in the other soils. The organic plasma is more black than brown in color and is more intensely developed than that which occurs in Zone I of Treatment 2 in the same soil. Most likely its composition is dominantly decomposed and humified litter which has been ingested and transformed by *L. terrestris*. Because the epigeous species do not ingest significant amounts of litter plasma development is not as intense in Treatment 2 of the Ellerslie soil.

The mixing of litter into the soil matrix by *L. terrestris* in the presence of clay(Plates 5b,5c) has led to the development of unistrial plasma fabrics(Table 8). The upper zone(U) of the midden in the Cooking Lake soil(Plate 5b) is characterized by the presence of phytogranic units admixed with matrix material(Plate 6a). As the excrement aged(lower portion of the midden -(L)) the phytogranic units decomposed and humified resulting in the unistrial plasma fabrics observed(Plate 9c). The plasma fabric descriptions indicate *L. terrestris* caused strong orientation of clays in the same manner as the epigeous species. The degree of orientation in the faecal material is likely stronger than the fabric descriptions imply as much of the fabric is masked by the organic plasma. Treatment of faecal material with H_2O_2 in the Ellerslie soil removed organic plasma concentrations revealing strongly oriented clays that have an omnisepic fabric(Plate 10).

Octolasion tyrtaeum,Aporrectodea turgida and *Lumbricus terrestris*(Treatment 4)

Alterations to plasma fabrics and related distribution patterns of the F-matrix and F-members are similar to those observed in Treatment 3 except

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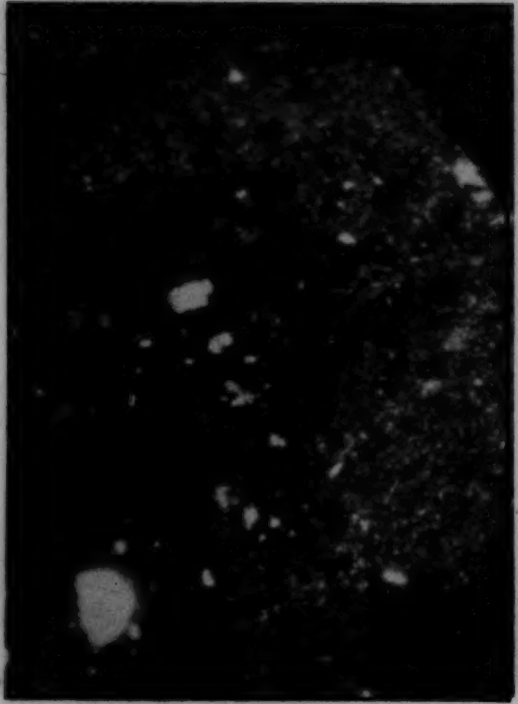


Plate 10a: Zones of humified plasma centrally located in faecal deposits. 20X.

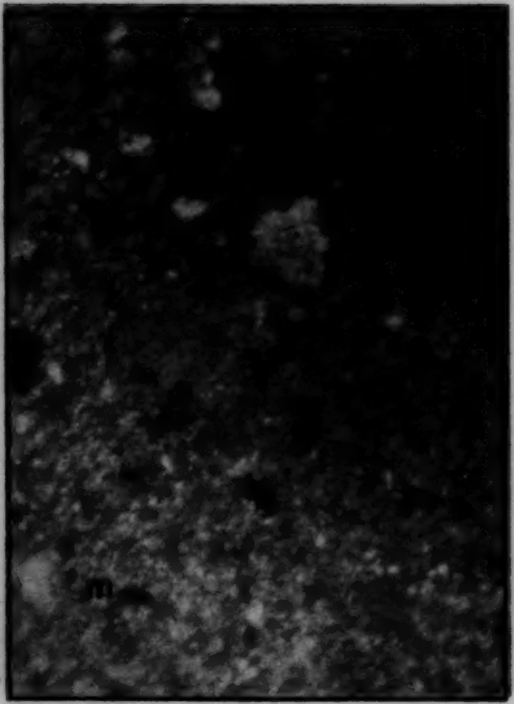


Plate 10b: Same zone as in Plate 10a. 80X.

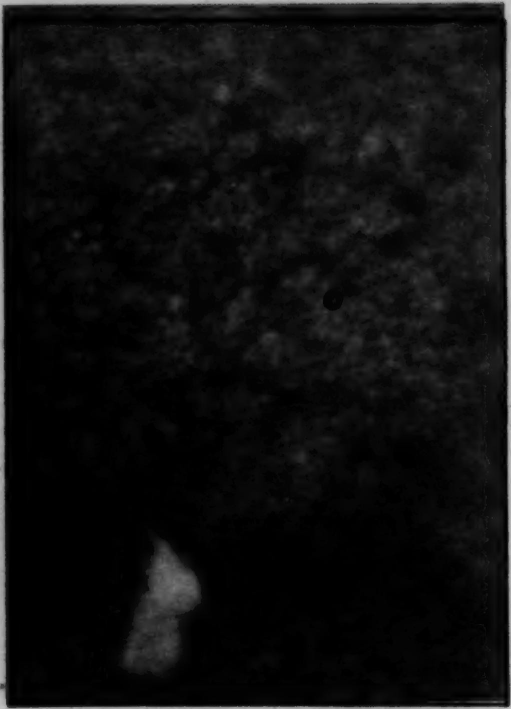


Plate 10c: Same zone as in Plate 10b after treatment with H_2O_2 to reveal omnisepic plasma fabric. 80X.

Legend
m) matrix. h) humified plasma.

Plate 10: Micrographs of plasma fabrics occurring in faecal material of *L. terrestris* (Ellerslie soil). crossed polarizers.

that the epigeous species appear to have accelerated processes initiated by *L. terrestris*.

Net positive benefits in terms of granular structure development were realized in the Spruce Grove(sandy loam) and Ellerslie(silty clay loam) soils(Plate 5a,Zone I and (c);Plate 5c,Zone I). In the Cooking Lake soil(clay loam) the degree of fusion of soil material is enhanced further than that occurring in Treatment 3(Plate 5b,Zone I). The most obvious changes to fabrics occur at the surface in Zone I of all three soils. The soil was worked over to the greatest extent in this zone by both ecological groups since faecal material was deposited by *L. terrestris* on the soil surface which is the region where the epigeous species were most active. Faecal deposits of *L. terrestris* are comprised of comminuted litter admixed with matrix material and as such provides an attractive substrate for the epigeous species.

Zone I in Treatment 3 of the Spruce Grove soil which is characterized by a dominantly porphyric fabric is absent in this treatment(4). Epigeous species have ingested the porphyric material and transported it into the bulk of the soil material resulting in a mixed separated fabric(Table 9). Soil components in the faecal material of *L. terrestris* are strongly bound together. After this material was ingested and moved by the epigeous species the strength of binding was retained so that excreted faecal material occurs more commonly as discrete units(Zone III (c))than where the epigeous species were active alone(Treatment 2). The loss of a distinct zone dominated by the presence of organic plasma may also have resulted from its decomposition by epigeous species using the plasma as a source of organic substrate.

The presence of a higher proportion of clay and lower proportion of sand in the Ellerslie soil and the interaction of the two groups of earthworms has led to the development of a dominantly matrigranic fabric in Zone I(Plate 8c). The presence of Zone II which is similar to Zone I in Treatment 2, the redistribution and reshaping of the midden formed by *L. terrestris* into matrigranic units and decrease in metavughs and channels in Zone III relative to Zone II in Treatment 2 indicates the activity of the epigeous species was concentrated at the soil surface. This likely reflects their preferential utilization of *L. terrestris* faecal material as a substrate. In the absence of a high proportion of sand to induce mucoid secretions the organic plasma likely originated from decomposed and humified litter.

In the Cooking Lake soil the fusion of the soil matrix likely results from processes similar to those described for Treatment 3. In this case fusion appears more extreme since epigeous earthworms have broken down the middens of *L. terrestris* so that the fused soil occurs across the entire soil surface.

4.2.1.10 Summary

In the introductory remarks it was stated that two forces, formation and stabilization, must be active in order for structural development to proceed. If agents or processes are active which could result in stabilization but no mechanism is present to form aggregates, no observable or lasting change to soil structure will occur.

Allison(1968) attributed the development of a highly stable granular structure under grasslands to the ability of their rooting system to simultaneously facilitate formation and stabilization of aggregates. The growth of roots provides the physical forces necessary to compress soil components together forming aggregates and the physical presence of the roots reduces inter-aggregate forces while providing a continual supply of organic matter which ultimately decomposes and complexes with inorganic components. An analogy may be drawn between the action of the rooting systems and that of earthworms. Tunnelling and ingestion of both organic and inorganic matter provides a mechanism for bringing both soil components into intimate contact with one another while transformations of organic matter within the gut or immediately after egestion enables it to complex with inorganic components. Thus the activities of earthworms can be very important to structural development in ecosystems where extensive rooting systems do not occur.

Results from the micromorphological study clearly demonstrate that earthworms cause alterations to soil structure but the type of changes observed are dependant on the species of earthworms and the nature of the soil in which they exist.

L. terrestris played a primary role in structural development by ingesting unaltered organic matter(litter) and bringing it into intimate contact with inorganic soil components. The organic matter may be decomposed, outside or within the gut of the earthworm, into forms capable of binding with the inorganic fraction. Although alteration to soil fabrics by *L. terrestris* were profound they occurred only on a localized basis.

Octolasion tyrtaeum and *Aporrectodea turgida* played a secondary role in structural development. They ingested small quantities of litter but large amounts of matrix material which was physically altered and translocated which resulted in homogenization of the soil. A synergistic effect in terms of structural development occurred when both groups of earthworms were active together. *L. terrestris* played the primary role of initiating the mixing and binding of organic and inorganic constituents. Epigeous species played the secondary roles of intensifying the processes initiated by *L. terrestris* and transporting the modified material into the bulk of the soil.

Organic plasma formed through the activities of earthworms bind soil particles together. Inference from the literature implies that an increase in secretion of bodily mucopolysaccharides occurs as a result of the aggravating presence of a high proportion of sand in the soil. In this study soils possessing a high proportion of sand were fused together by organic plasma in such a manner that porphyric fabric types develop. It is thought that this fusion of soil components under the influence of earthworms results from the secretion of mucopolysaccharides. When contributions to organic plasma originated from the decomposition of plant material, enhanced by ingestion of litter by surface feeding species(*L. terrestris*), faecal material occurred more often as discrete units leading to fragmoidic or granoidic fabric types.

All species of earthworms used in this study caused alterations to plasma fabric types. Where clays were present the degree of their separation and orientation invariably increased. This is attributed to earthworms subjecting matrix material, occurring in a semi-liquid state within the gut, to compressive forces during or after passage through the gut. Unistrial fabrics were observed in faecal deposits of *L. terrestris*. These fabrics likely resulted from oriented clays being admixed with elongated phytogranic units which decomposed to organic plasma in situ. These interactions of earthworms and soil produced different fabric types depending on the texture of soil and species of earthworms involved.

Where sand sized particles dominated the soil texture and the occurrence of clays was minimal the net effect on soil structure from ecological groups acting individually or together was a positive one. Binding of soil particles through the action of either group of earthworms alone resulted from organic plasma largely originating from mucoid secretions. The resulting fabric types in worm-worked zones are dominantly porphyric. Where *L. terrestris* was active alone some faecal material occurs as discrete units reflecting binding by organic plasma originating from decomposed and humified litter. Where both ecological groups were active together faecal material occurs throughout the soil matrix as discrete units. Organic matter introduced to the soil matrix by *L. terrestris* became available to the epigeous species which ingested not only the new source of organic matter along with mineral soil components but also that material already modified by *L. terrestris*. Inorganic soil components bound by both sources of organic plasma were mixed into the bulk of the soil material by the epigeous species resulting in homogenization of the soil and in an increase in contact between inorganic and organic components.

When both sand and clay were present in significant proportions different fabric types developed under the influence of the same species of earthworms. Mucoid secretions were still induced by the presence of the sand fraction but the presence of clays(oriented through the action of earthworms) for combining with the plasma resulted in fusion of the soil matrix. Where *L. terrestris* was active unistrial masepic fabric developed resulting from the admixing of elongated phytogranic units with oriented clays. Some faecal pellets occur as discrete units in the region where organic plasma concentrations originated from humified litter. Where both ecological groups were active together the fusion of soil material is more pronounced since the epigeous species enhanced processes intiated by *L. terrestris*.

Where clay and silt dominated the soil texture sand did not occur in high enough proportions to aggravate excessive mucoid secretion. Where *L. terrestris* was active alone binding of soil aggregates resulted primarily from plasma originating from decomposed and humified organic matter intimately combining with oriented clays. Faecal material deposited on the soil surface occurs more frequently as discrete units than in the clay loam soil. When both species were active together processes leading to the formation of discrete faecal units were accelerated resulting in a zone of phyto-matrigranic fabric on the soil surface.

In all soils examined tunnelling activities of the geophage species resulted in numerous smooth metavughs and channels occurring throughout the soil volume as the earthworms literally "ate" their way through the soil. The channels are discontinuous and likely do not aid in the drainage of free water. This tunnelling activity increased in importance in soils which were highly compacted. Channels produced by *L. terrestris* are long, vertically oriented and opened to the surface and probably aid in the drainage of free water. In the fine textured soils compression features occur around the metavughs and channels resulting from *L. terrestris* activity. These features reflect the inability of this species to "eat" its way through the soil. Tunnels are created by the earthworm pushing and forcing its way through the soil.

Most channels and metavughs produced by both ecological groups are characterized by colloidal material occurring around their edges. Where *L. terrestris* was active more organic plasma is present in the tunnel linings. These colloidal materials occur in association with channels that direct the flow of water and may be effective in increasing the retention of water in the soil.

4.2.2 Earthworms and Stabilization of Soil Structure

4.2.2.1 Introduction

Numerous mechanisms have been proposed to bring about the stabilization of soil structure. These have been reviewed in detail by Harris et al.(1966). It has been demonstrated by many researchers that the faecal material of earthworms is more stable than aggregates in soils where they were not active(Teotia et al.,1950;Hopp et al.,1946;Piearce,1981;Van Rhee,1977), yet few efforts have been made to relate this back to the proposed mechanisms for stabilization.

Of the plethora of research conducted in the area of stabilization mechanisms the role of carbohydrates such as polysaccharides and uronic acids in binding with clays has received the most attention and widespread acceptance(Harris et al.,1966; Hepper,1975;Greenland et al.,1975;Cheshire,1979). Polysaccharides and uronic acids in the soil may originate from plant or microbial cellular components as well as extracellular secretion from plant roots and microorganisms(Fazio et al.,1981; Cheshire,1979). The majority of the available literature indicates that it is the carbohydrates of microbial origin which are most important in the stabilization of soil structure (Marshall,1976;Flaig et al.,1977; Cheshire,1979). Earthworms are also known to alter both the qualitative and quantitative balance of the microbial community dramatically (Parle,1963b;Dawson,1947; Day,1950;Atlavinyte et al.,1970;Loquet et al.,1977). Most likely the influence of earthworms on aggregate stability in regards to carbohydrates is an indirect one through their effect on the microbiological community. In view of the attention given to polysaccharides and uronic acids and their role in aggregation, analyses for these constituents were done in this study on the faecal pellet, tunnel lining and unaltered parts of the soil to determine if earthworms enhance their production and binding with clays. A stepwise extraction procedure was used as described in Chapter 3 in order to faciliate a physico-chemical separation of neutral sugars and uronic acids into three components as follows.

1. free or weakly organically bound component
2. clay-bound component
3. residual component

Since microorganisms and their metabolic products are stongly implicated in aggregate stabilization the study was augmented with total plate counts using faecal and control soil materials. Results from the micromorphological portion of this study showed that intimate association of organic and inorganic plasma resulted from the activities of earthworms. In order to examine the role of earthworms in organo-clay complexing further and to augment the carbohydrate analysis , X-ray diffraction patterns were conducted on the <2um fraction of the control and faecal soil materials before and after treatment with H_2O_2.

4.2.2.2 Uronic Acids

No uronic acids were detected during the analysis of all the faecal and approximately half of the tunnel lining and control samples. This suggests that stabilization of aggregates through the action of earthworms does not result from enhanced production of uronic acids. Cheshire(1979) stated the idea that aggregate stability is related to the uronic acid concentration in the soil has been tested frequently but the results have been inconsistent. Parfitt and Greenland(1970) found that the uronic acid component of a soil polysaccharide was adsorbed by montomorillonite only if Al ions or hydroxy aluminum species were present at a low pH. Conversely adsorption of the neutral sugar component was independent of the pH and type of cations present. At a pH above 3.2(pK of uronic acids) galacturonic acid would be largely dissociated. The resulting coloumbic interaction between the negatively charged clay surface and the ion would prevent adsorption(Parfitt and Greenland,1970). Such forces likely prevented adsorption of uronic acids to clays in the soils used in this study. The pH of all samples (Appendix VIII) were well above the pK for uronic acids. This explains the absence of uronic acids in the clay-bound component but not the residual or free components where the potential for binding with exchangeable cations could exist. It is also possible that the concentration of uronic acids in the samples analyzed was below the detection limits of the procedure used. Although estimates of uronic acids are available in the literature it is difficult to use these data to extrapolate the concentrations expected to be present in the samples used in this study. In the other studies many different extraction and analytical procedures were used on soils which were typically high in organic matter. If the values found in the literature for the relative proportion of uronic acids and neutral sugars were used as an index, a crude estimate can be made for the expected concentration of uronic acids relative to the concentration of neutral sugars which were detected in the samples analyzed. In the literature the ratio of uronic acids to neutral sugars ranges from 0.2:1 to 0.5:1(Cheshire,1979). Using the widest ratio(0.2:1), uronic acids should have been detected in faecal pellet samples where neutral sugar concentrations were in the range of 2000-3000 ug glucose eq /gram of soil, since the detection limit for the procedure used was 200 ug glucose or galacturonic acid eq /g soil. The major factor controlling the detection limit in the procedure was sample size. Since the amount of faecal material collected was small relative to the number of analyses performed only one gram samples were available for this analysis. If a lower detection limit is to be achieved a larger size of sample should be used in the initial extraction step of the procedure.

4.2.2.3 Neutral Sugars

Statistically significant differences in the concentration of neutral sugars were found between parts(soil,tunnel linings,faecal pellets) and between components(free,clay-bound and residual neutral sugars). In some cases differences in neutral sugar concentrations of the aforementioned occurred as a result of soil texture, species of earthworms as well as an interaction of the two.

Initially it was desireable to make comparisons of the neutral sugar concentrations between all treatments, components and soil textures for the unaltered soil material(Table 10) for the following reasons:

1. To test the efficiency of separating the faecal material and tunnel linings from the unaltered soil material in Treatments 2, 3 and 4. If the separation was efficient values for the unaltered soil material in Treatments 2, 3 and 4 should not differ drastically from those in the controls(Treatment 1 and 5).

2. To provide a comparison of the inherent neutral sugar concentrations between the soils of different textures(Treatment 5). This would indicate if differences in neutral sugar concentrations resulting from the interaction of species with soil texture were real and not the result of inherent differences between parent materials.
3. To provide a sound basis for making further statistical comparisons at the parts, parts x species and parts x species x texture levels of interaction. Proper statistical analysis at these levels in Treatments 2, 3 and 4 depends on the absence of significant or inexplicable differences between the unaltered soil material when comparisons are made with the contols.

No statistically significant differences in the concentration of neutral sugars were found between the textural classes in Treatment 5(Table 10). All parent materials had consistantly low inherent levels of neutral sugars permitting valid comparisons at the interaction levels. The concentration of neutral sugars in the residual component of Treatment 1 was consistantly higher for all soils relative to Treatment 5 and the other components. This most likely represents organic constituents which were physically translocated from the grass into the soil during the leaching process. In Treatments 2, 3 and 4(earthworms present)

Table 10:Neutral sugars(glucose eq ug/g soil) for the unaltered soil from all treatments,components and soil types.

SOIL TYPE	NEUTRAL SUGAR COMPONENT	TREATMENT NUMBER				
		1	2	3	4	5
SPRUCE GROVE	FREE	a 0	a 0	a 0	a 0	a 230
	CLAY BOUND	a 0	a 95	b 390	a 0	a 0
	RESIDUAL	b 382	a 0	a 0	a 0	a 0
COOKING LAKE	FREE	a 0	a 0	a 314	a 286	a 0
	CLAY BOUND	a 0	a 244	a 0	a 0	a 0
	RESIDUAL	b 1110	b 1130	ab 656	a 215	a 0
ELLERSLIE	FREE	a 0	a 93	a 0	a 0	a 0
	CLAY BOUND	a 0	a 0	a 92	b 275	a 0
	RESIDUAL	b 306	a 116	a 0	a 0	a 0

the concentration of neutral sugars in the residual components was reduced. Organic constituents which were retained in the mineral soil in the absence of earthworms were subjected to ingestion and enhanced decomposition in their presence. The trend across Treatments in the residual component of the Cooking Lake soil is particularly interesting since it reflects the function of different ecological groups of earthworms in the decomposition process. In Treatment 2 the concentration of neutral sugars is similar to that in Treatment 1. Litter accumulated on the soil surface and was not ingested to a significant degree by the geophages(Table 11). Therefore the opportunity existed for organic constituents to be introduced and accumulated in the mineral soil in a similar fashion to that found in Treatment 1. In Treatment 3 *L. terrestris* completely removed litter form the surface(Table 11) and concentrated it within the faecal material. Consequently less organic constituents were washed into the bulk of the soil and neutral sugar concentrations in the residual component were lower. Where both groups of earthworms co-existed(Treatment 4) decomposition of the organic constituents was more complete and organic matter remained concentrated in the faecal material. The neutral sugar concentration in the unaltered soil material remained comparable to that found in Treatment 5. Why this condition is observed for the Cooking Lake soil and not the others is explained in more detail in Section 4.3.4.

In general the neutral sugar concentrations in the unaltered soil material from Treatments 2, 3 and 4 were not statistically or inexplicably different from the controls. Further statistical comparisons at the parts and interaction levels are valid. The concentrations in two instances(clay-bound component-SG(T.3)-E.(T.4)) were significantly higher than in the controls. Since these differences do not exhibit a consistant trend across treatments and components they likely reflect a poor separation of the parts during sampling. These aberrations are not considered problematic for subsequent interpretation of data at the parts and interaction levels.

Data for neutral sugar concentrations in the free and residual components showing the interaction of soil type with parts are presented in Figure 6. Concentrations of free neutral sugars exhibit a similar trend in each soil type(texture). No significant differences in the concentrations of free neutral sugars resulted from a further interaction with species of earthworm. Regardless of soil texture or species of earthworm neutral sugar concentrations in the faecal material are always significantly higher than concentration in the tunnel linings or unaltered soil material. Concentrations in tunnel linings and soil are always low and not

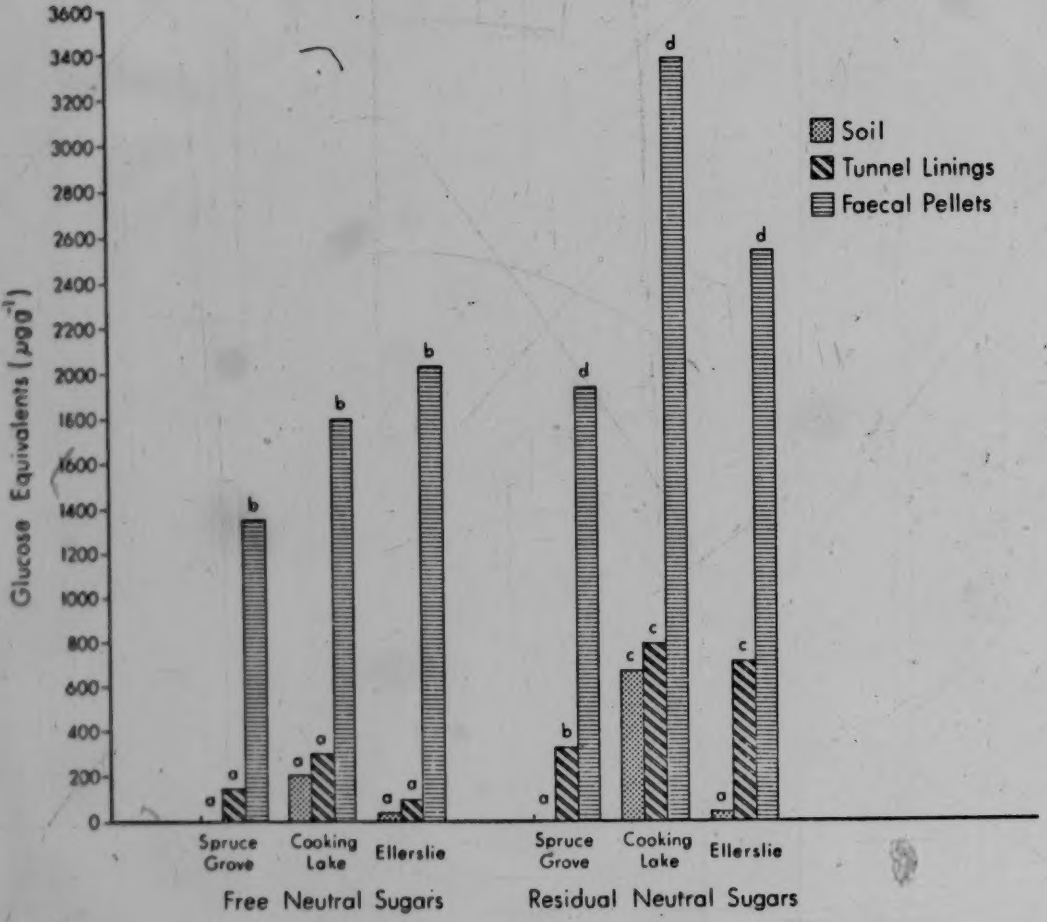


Figure 6:Distribution of free and residual sugars(ug glucose eq/g soil) between soils and parts(a-d significantly different, P=.05).

significantly different. The free neutral sugar component in this study roughly corresponds to fulvic acid-A extracted in the procedure used by Anderson et al.(1974). This component is likely dominated by simple sugars released upon decomposition of the added grass which is accelerated in the faecal material through the influence of earthworms on microorganisms(discussed in section 4.3.3.).

The residual component exhibits trends similar to those in the free component except concentrations of neutral sugars in the tunnel linings are significantly higher than in the unaltered soil for two of the three soil types(Fig. 6). The residual component in this study roughly corresponds to the humic acid plus humin fraction in the classical extraction techniques used to characterize organic matter(Anderson et al.,1974). Thus the residual component would be dominated by high molecular weight polyaromatic organic compounds having a complex structure which are resistant to microbial attack as well as cellulose and other resistant forms of soil carbohydrates(i.e. plant fragments).The extraction procedure does not distinguish between the relative proportions of neutral sugars occurring in the humic acid or humin fractions. Micromorphological examination of the thin sections suggests both plant fragments(phytogranic units) and humic materials(organic plasma) are present in the faecal material. Most likely contributions from both sources combined to give the very high values for neutral sugars in the residual component of the faecal material.

The clay-bound component of the neutral sugars is of primary interest in this study since the binding of clays with polysaccharides is considered important to the stabilization of soil aggregates. Results from this analysis are strikingly consistant with the micromorphological observations(Fig. 7). In every case except one the statistically significant highest concentrations of clay-bound neutral sugars occur in the faecal material of soils where metafragmoidic or mullgranic fabric were observed. The exception is the high concentration of clay-bound neutral sugars in the tunnel linings of the Cooking Lake soil where both ecological groups of earthworms co-existed(Treatment 4). In this soil an increasing degree of fusion within the soil matrix was observed from Treatment 2 through Treatment 4. The trend showing an increase in degree of fusion is associated with a trend that shows a decrease in concentrations of clay-bound neutral sugars in the faecal material where the fusion occurred. The greatest degree of aggregate formation occurred in the Ellerslie soil. In all treatments for this soil the concentrations of clay-bound neutral sugars are consistantly higher in the faecal material than in the tunnel linings and unaltered soil. In the Spruce Grove soil the greatest degree of fusion of the soil matrix occurred in Treatment

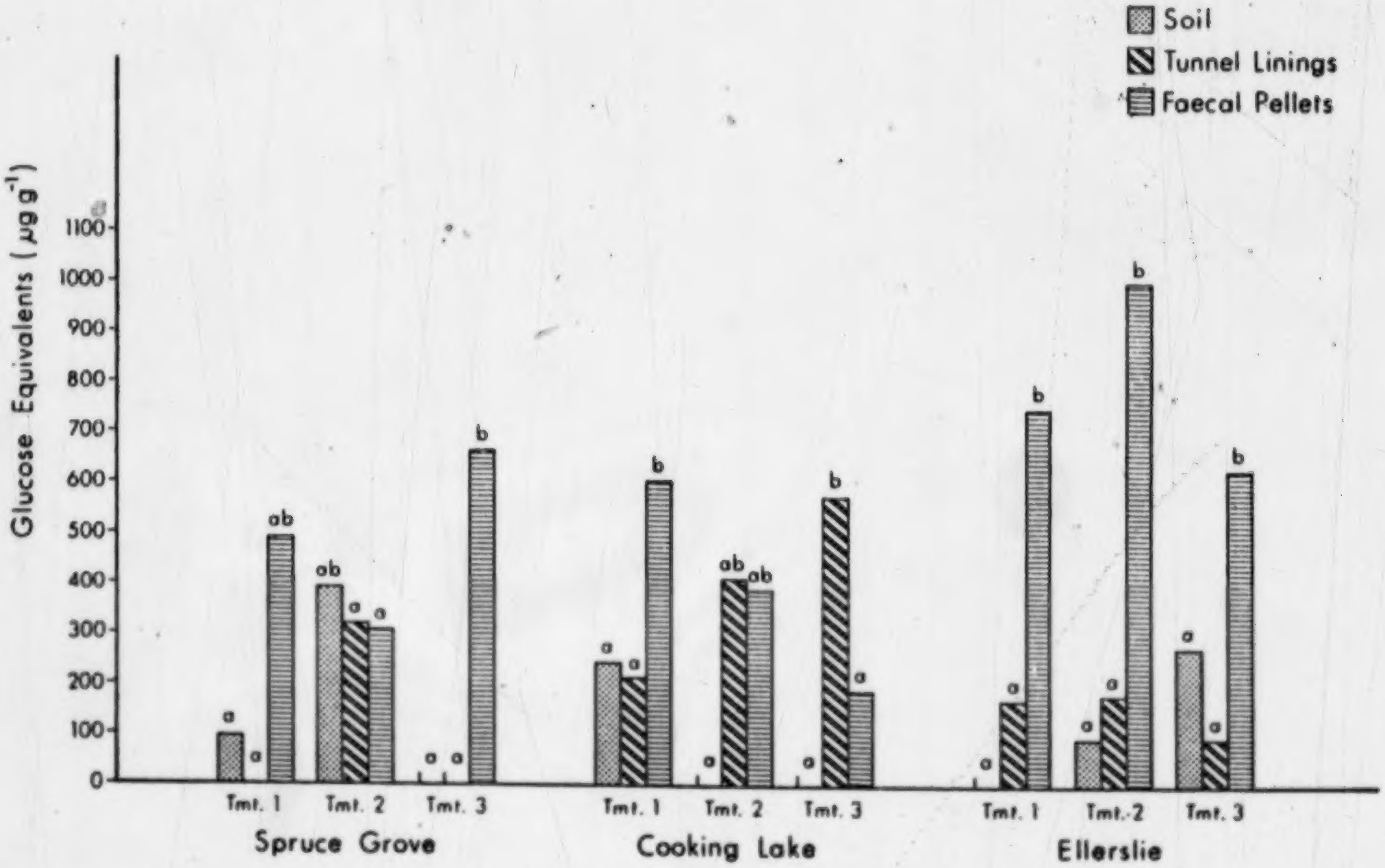


Figure 7:Distribution of clay-bound neutral sugars(ug glucose eq/g soil) between treatments, soil types and parts. (a-b significantly different, P=.05)

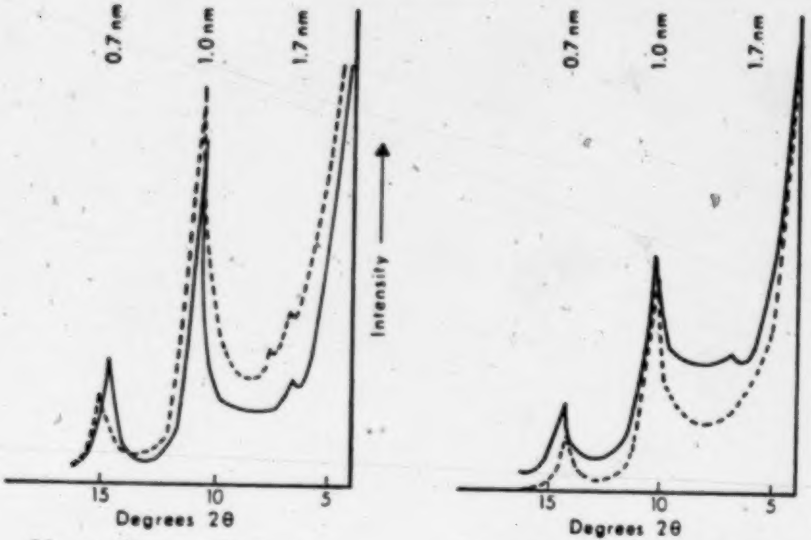
3(*L. terrestris*). The concentration of clay-bound neutral sugars is lower in the faecal material of *L. terrestris* than in the faecal material from Treatments 2 and 4. Of the latter two treatments the concentration of neutral sugars is highest in Treatment 4 where the greatest degree of aggregate formation occurred in this soil type.

These data strongly support the concept that the enhanced production of neutral sugars and their binding with clay is a key mechanism for the stabilization of aggregates formed by earthworms. The mechanism through which earthworms enhance binding of clays with polysaccharides is most likely one in which inorganic and organic constituents are brought into intimate contact during ingestion and passage of soil through the gut. After excretion the faecal material is enriched with microflora. In general total microbial populations were found to be considerably higher in the faecal material than in the control soil(Figures 10-12). Decomposition of organic residues is enhanced in the faecal material and resultant polysaccharides are available for complexing with clays already in intimate contact with organic substrates. The preferential enrichment of bacteria such as *Cytophaga* sp.(Fig.11) in the faecal material suggests conditions exist in the castings that are condusive to the breakdown of resistant organic materials. Isolates of *Cytophaga* sp. from the faecal material of *L. terrestris* showed lytic capability against chitin, casein and mannan. Indications are that cellulose is degraded by some of these isolates but results were inconclusive(Table 15).

Low concentrations of neutral sugars in the faecal material are associated with adverse soil structure where fusion of the soil matrix occurred. This association occurred only in the Cooking Lake soil(Treatment 3,4) and where *L. terrestris* was active alone in the Spruce Grove soil. Data presented in Section 4.3.4 indicates that decomposition was greatly accelerated in the Cooking Lake soil in the presence of *L. terrestris* and that the Cooking Lake soil, in general, had a low capacity for stabilizing organic matter through binding with clays. The combination of these factors led to high net losses of carbon in the Cooking Lake soil and the development of poor structure. Conversely data presented in Section 4.3.4 indicates that when *L. terrestris* was present alone in the Spruce Grove soil decomposition was significantly retarded. Therefore, low amounts of organic constituents in forms capable of binding with clays were introduced to the soil. Possibly this, in combination with mucopolysaccharide excreted from the earthworms body(as suggested in Section 4.2.1) combined to produce the fused structure observed in the Spruce Grove soil in the presence of *L. terrestris*.

4.2.2.4 X-ray Diffractometry

The <2um fractions from the control soils and faecal pellets from Treatment 2(*O.tyrtaeum/A.turgida*) and Treatment 3(*L. terrestris*) for all three soil types were analyzed by X-ray diffractrometry before and after treatment with H_2O_2 to oxidize organic matter. X-ray patterns from faecal pellet samples of *O.tyrtaeum/A.turgida* had a sharp .995nm peak similar to the controls(Fig.8) Although the diffraction analysis indicated that the clay separates from the *L. terrestris* faeces were identical to the controls following oxidation of the organic matter, distinct differences are observed in the X-ray diffraction characteristics of the expandable clay minerals prior to the oxidation treatment. This is illustrated(Fig.8) by the marked broadening of the 0.995nm peak of the untreated separates in the 1.3-0.995nm region. In considering the nine treatments analyzed(3 controls, 6 faecal pellet samples from different combinations of soils and species of earthworms) this phenomenon occurred only in samples where fusion of the soil matrix was observed in thin section and where neutral sugar concentrations were low in the faecal pellets(Treatment3-Cooking Lake and Spruce Grove soils). This indicates some organic molecule other than neutral sugars is preventing the collapse of expandable clays. It may also be related to the fusion of the soil matrix.

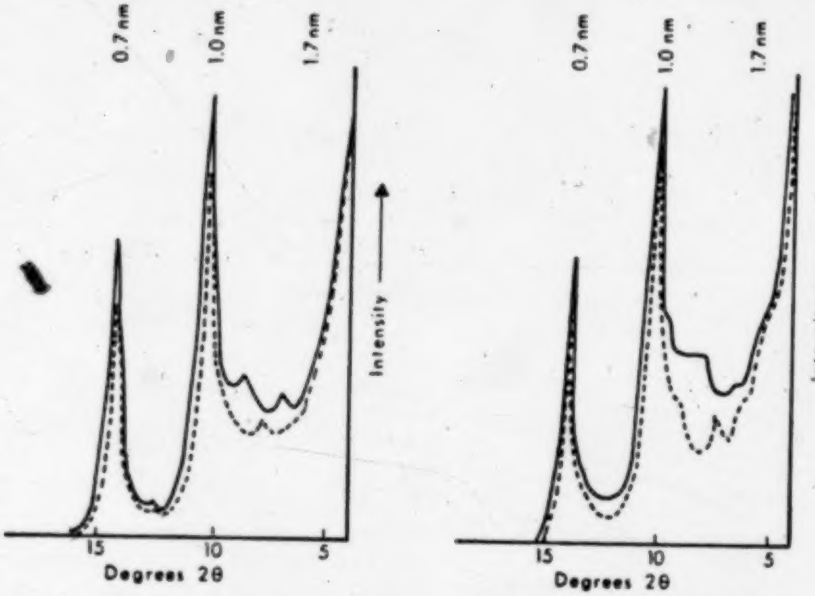


Spruce Grove - Control

Spruce Grove - Faecal Pellets

— Before H_2O_2

---- After H_2O_2



Cooking Lake - Control

Cooking Lake - Faecal Pellets

Figure 8:X-ray diffraction patterns of the <2um fraction from the controls and faecal pellets of *L.terrestris* before and after treatment with H_2O_2 (K-saturated, 0 R.H.)

It has been shown that entire protein molecules are capable of entering the interlamellar space of montmorillonite clays(Theng,1979). Although data exist suggesting polysaccharides behave similarly to proteins the molecules are usually too large to enter the interlamellar space of expanding clays. Frequently only partial expansion is observed. Binding of polysaccharides with clays is more commonly thought of as being a surface phenomenon(Theng,1979). Proteinaceous molecules that originate from excretion through the body of earthworms(as suggested in Section 4.2.1) may possibly intercalate clay minerals and produce the observed fused structure. No doubt other mechanisms may also be active in producing the type of fused structure observed in some of the treatments. The effect that proteinaceous materials have on soil structure when secreted from the bodies of earthworms deserves further attention and study.

4.2.2.5 Summary

In this portion of the study an attempt was made to relate the development of soil structure through the activities of earthworms to mechanisms considered important to the stabilization of soil aggregates.

The presence of uronic acids was not detected in any of the samples analyzed suggesting their involvement in stabilizing aggregates formed by earthworms is of little or no importance. However, concentrations of neutral sugars in the faecal material were strongly related to structural development observed in the thin sections.

Three components of neutral sugars were extracted from the soils. These were free, clay-bound and residual. Concentrations of neutral sugars were almost always higher in the faecal material than in the control soils(Treatments 1,5) or the unaltered soil material where earthworms were present(Treatments 2-4). Neutral sugars in the free and clay-bound components are likely end products from microbial decomposition of litter. Neutral sugars in the residual component likely originate both from humified organic matter and undecomposed grass fragments.

Only the clay-bound neutral sugars were related to soil structure. In soils where metafragmoidic and mullgranic fabrics resulted from the activities of earthworms the concentrations of clay-bound neutral sugars were higher in the faecal material than in the control soils and unaltered soil and tunnel lining parts. In soils where the degree of fusion of the soil matrix was high the concentration of clay-bound neutral sugars in the faecal material was low.

The different trends in aggregate formation and concentrations of clay-bound neutral sugars were strongly related to the interaction of species of earthworms with soil type. Although it can be said from data presented in this thesis that earthworms can produce granular soil structure and this is related to the high concentration of clay-bound neutral sugars in the faecal material no conclusive data were collected to indicate why, in some cases, adverse soil structure is produced by earthworms. Fusion of the soil matrix appears to be related mainly to the activity of *L. terrestris*. Fusion of the soil matrix in the Cooking Lake soil may be related to *L. terrestris* accelerating decomposition which resulted in high net losses of soil organic matter(Section 4.3.4). It has also been suggested that mucopolysaccharide secretions from the bodies of earthworms may be involved in the development of adverse soil structure.

4.3 Earthworms and Decomposition

4.3.1 Introduction

It is frequently stated or implied in the literature that earthworms accelerate decomposition. This conclusion has been largely based on the observations that earthworms mix litter into the mineral soil, which would otherwise accumulate on the soil surface. Earthworms also often increase the number of microorganisms in the soil. Although these observations hold true in some cases data presented in this thesis shows that in other cases earthworms do not mix substantial amounts of litter into the soil and that they do not always increase the number of microorganisms present. It will also be demonstrated that the consequence of these processes is reflected in very different trends for the nature and accumulation of organic matter in the soil depending on the species of earthworm and type of soil involved.

4.3.2 Organic Matter Additions

Data presented in Table 11 shows the percent of grass added to the columns which was not recovered at the termination of the experiment. Grass not recovered was probably decomposed or physically removed from the surface in the case where earthworms were present. Results are consistant with the literature in that more organic matter was not recovered in the presence of earthworms(Treatments 2-4). The higher loss of organic matter in Treatments 3 and 4 than Treatment 2 reflects the feeding habit of *L. terrestris* which removed almost all of the grass from the surface and pulled it down into the mineral soil. Conversely the loss of surficial organic matter in the presence of the geophages was far less since their feeding habit is not condusive to the physical removal of substantial amounts of litter from the surface.

Table 11:% Reduction in weight of grass added to the soil surface

Treatment Number				
1	2	3	4	5
a 57	b 73	c 94	c 94	N/A

values not preceeded by similar letters are significantly different P=.05

The interaction of species of earthworm with soil type resulted in no difference in the amount of organic matter removed, yet significant differences in the fate of organic matter were present as a result of these interactions. These differences in the fate of organic matter will be discussed in Section 4.3.4.

4.3.3 Microbiology

Data presented in Figures 9-11 demonstrate that earthworms influence the quantitative and qualitative balance of the microbial community in the soil. The shift in this balance varies depending on the species of earthworm and nature of the microbial community inherent to the soil. It is sometimes suggested in the literature that the frequently reported increase in microbial numbers in faecal material is simply related to the increased availability of organic substrates mixed into the soil by earthworms(Bal,1982). Data presented here and in the

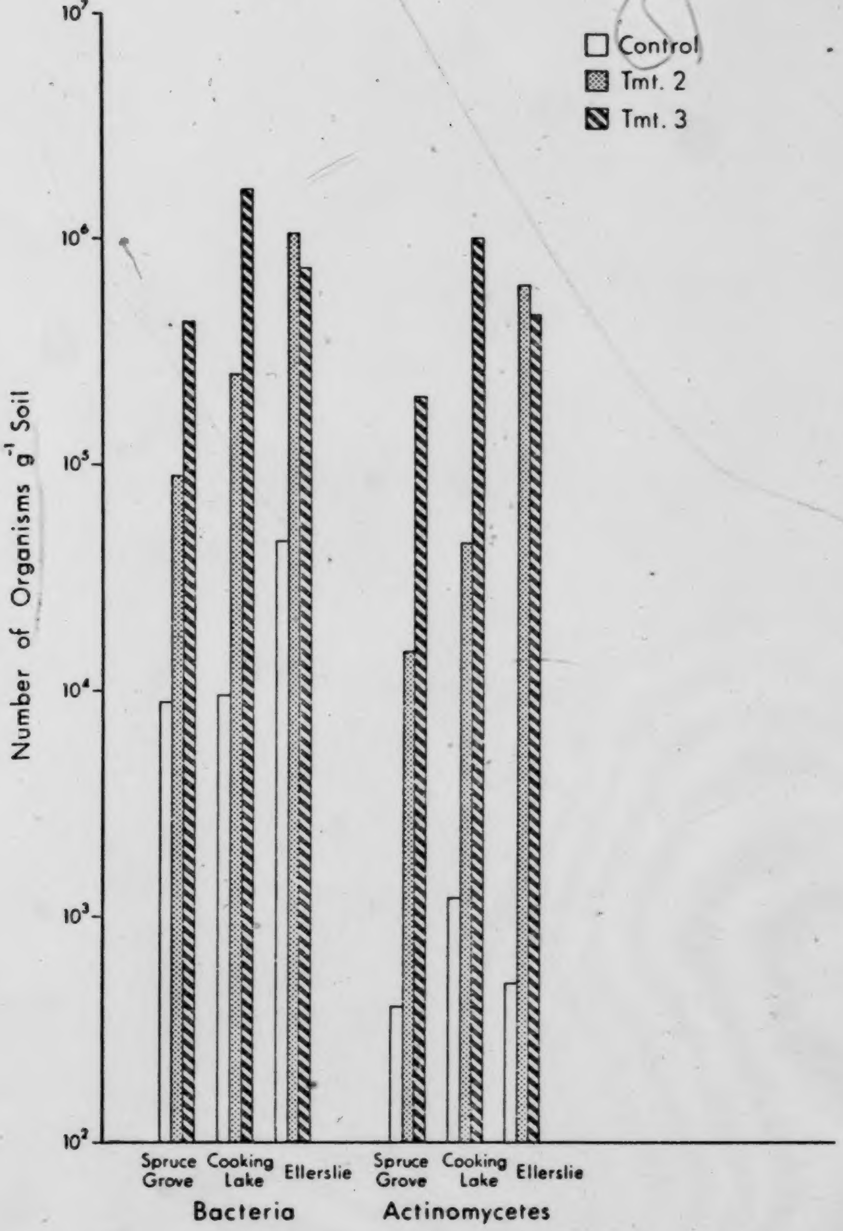


Figure 9:Bacteria and Actinomycetes(#/g soil) in the controls(C) and faecal pellets of *O.tyrtaeum/ A.turgida*(2) and *L.terrestris*(3).

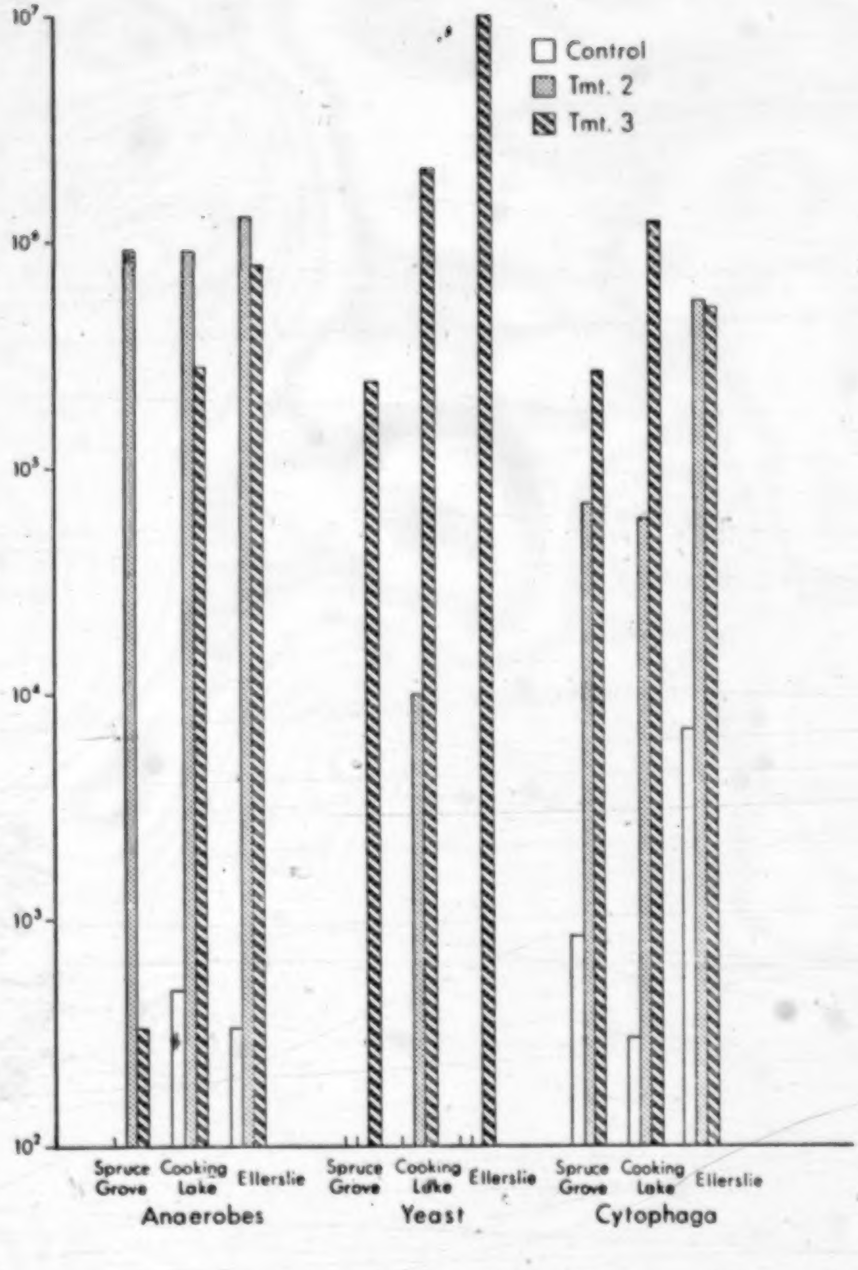


Figure 10:Anaerobes, Yeasts and *Cytophaga* sp.(#/g soil) in the controls(C) and faecal pellets of *O.tyrtaeum/A.turgida*(2) and *L.terrestris*(3).

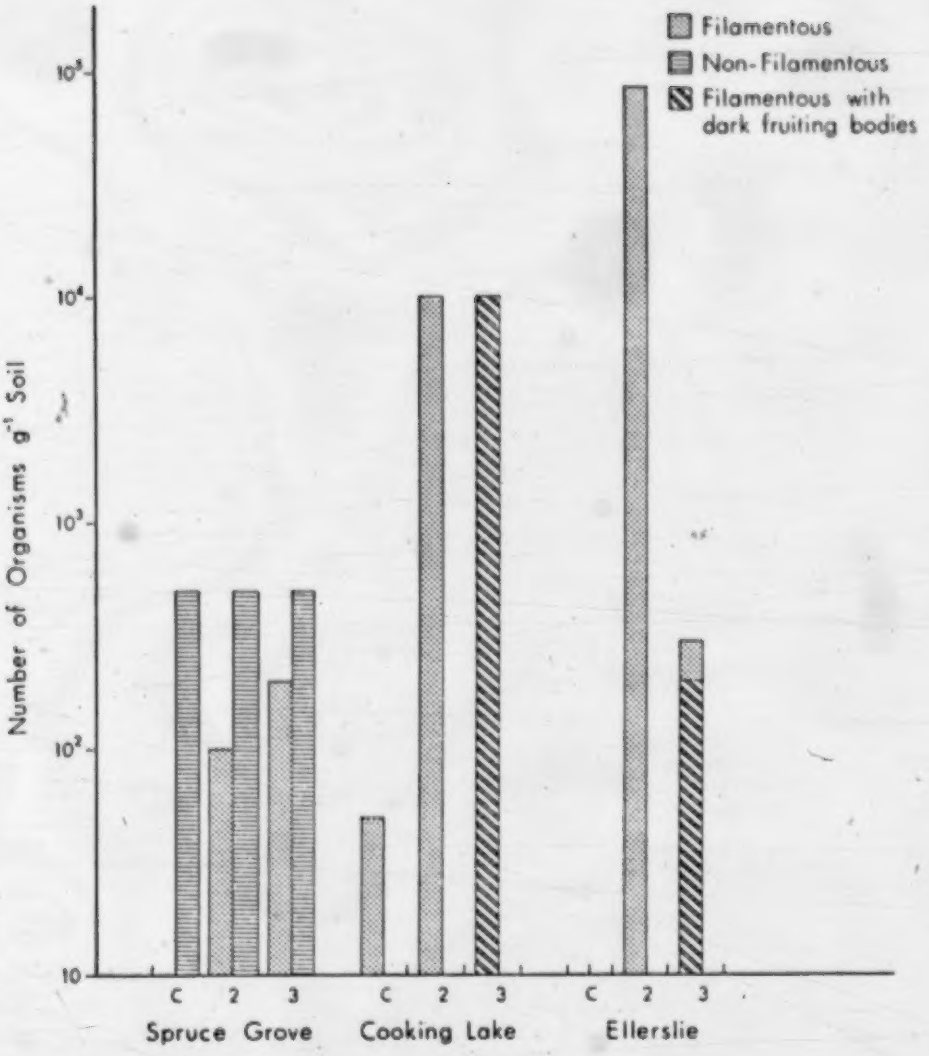


Figure 11:Forms of Fungi(#/g soil) in the controls(C) and faecal pellets of *O.tyrtaeum/A.turgida*(2) and *L.terrestris*(3).

literature suggest this is not true and that the influence of earthworms on the microbial community is more direct and selective.

Although *L. terrestris* introduced considerably more organic matter into the soil than *O. tyrtaeum/A. turgida* (Table 11) this was not always reflected in higher numbers of microorganisms in their faecal material(Fig. 9-11). In some instances(SG-anaerobes;E-fungi) numbers are lower in the faecal material of *L. terrestris* as compared with *O.tyrtaeum/A.turgida*. In other cases (mainly Ellerslie soil) the number of organisms in *O.tyrtaeum/A.turgida* faecal material are as high as those in *L. terrestris* faecal material even though they introduced less organic matter into the soil. These data lead to the rejection of the hypothesis that earthworms increase microbial numbers by introducing more organic substrate into the soil and accept the alternative hypothesis that enrichment or decline of specific groups of microorganisms results from a direct influence of earthworms on the microflora. This influence is most likely related to the feeding habits of the earthworms and their subsequent digestion of ingested materials.

The decomposition of digested litter is a unique case in which a symbiosis exists between the herbivore and the decomposing microflora. The herbivore provides a unique physico-chemical environment in its gut and excrement which ensures the continuation of the decomposer population, while the microflora and their metabolic end products provide nutrients and organic substrates which can be digested and assimilated by the herbivore.

Lodha(1974) discussed the processes and the symbioses involved in the decomposition of digested litter in ruminants and ruminant-like mammals. His discussion is briefly summerized in the following section in order to provide an understanding of these processes. Subsequently it will be proposed, using data collected in this study and supporting evidence from the literature, that decomposition of litter as influenced by earthworms is analagous to that of ruminants and ruminant-like mammals.

During digestion in ruminants simple carbohydrates are digested by intestinal juices while starch, hemicellulose, cellulose and lignin are digested through a symbiosis with microorganisms. Processes leading to the degradation of resistant carbohydrates in the gut are mainly anaerobic. The faeces provide an environment condusive to initiating the simultaneous activity of actinomycetes, bacteria, fungi and protozoa. Conditions in the excrement favourable to the activity of these organisms include;

1. The presence of a large quantity of readily available carbohydrates.
2. Increased availability of nitrogen due to bacteria and protozoa killed and digested in the intestine.
3. The excrement is rich in vitamins, growth factors and minerals. Coprogen, a factor essential to the growth and fruiting of many fungi, is found only in dung.

4. The excrement has a high moisture content and ability to retain water.
5. The pH of the excrement is around 6.5.
6. The structure of the faeces resulting from mastication favours good aeration.

Of all the decomposer organisms, the activity and proliferation of fungi preferentially adapted to dung is strongly favoured. These fungi not only prefer dung but have developed features which enable them to reappear in dung. Their spores are pigmented, strongly adhesive and are dispersed with a high velocity. This mode of dispersion increases the probability that the spores will be reingested by the herbivore. The spores are not injured during digestion. In fact the intestinal temperature and digestive juices break their domancy and stimulate germination in the excrement.

Thus two positive feedback processes are involved in the decomposition of digested litter. The first takes place in the gut and is dominated by anaerobic decomposition while the second takes place in the faeces and is dominated by fungal activity.

It is proposed in this thesis that digestion, and therefore decomposition, of litter by earthworms is similar to that just described for herbiverous ruminants and ruminant-like mammals. Supportive data from this study and the literature are summerized in Tables 12-14. In general data collected in this study agree with the proposed analogy

Table 12:Evidence for digestion in earthworms being analagous to ruminants

Data and Observations from this Study	Evidence in the Literature	*Relation to Ruminants
enrichment of anaerobes in the faecal material	enrichment of cellulolytic anaerobes in faecal material(Loquet et al.,1977)	anaerobes are the dominant miroflora involved in fermentation in the rumen.
	cellulolytic, butyric acid forming microorganisms associated with earthworms(Edwards,1974)	
	gut flora unique to earthworms known to exist Piearce et al.(1980)	microflora in the rumen are uniquely adapted to conditions in the rumen
earthworms ingest one anothers faeces	earthworms ingest one anothers faeces(Bal,1982)	mode of inoculum transfer between ruminants
presence of protozoa problematic in the study of nitrogen fixers	known association of earthworms with protozoa(Dixon,1975) known existence of protozoa unique to the gut of earthworms (Piearce et al.,1980) Protozoa instrumental to the nutrition of *E. foetida* (Miles, 1963)	Protozoa always associated with rumen microflora Function unknown but thought to be cellulolytic
enrichment of *Cytophaga* sp. in faeces of earthworms		*Cytophaga* sp. associated with numerous herbiverous ruminants.

*references
Stanier et al.,1970
Lodha, 1972

Table 13:Physico-chemical properties of earthworm faeces which are similar to ruminant faeces

Data and Observations from this Study	Evidence in the Literature	*Relation to Ruminants
Concentration of extractable glucose equivalents higher in the faecal material than control soils. Generally soluble organic carbon in leachates from columns where earthworms were present is greater than in the controls.		Presence of a large quantity of readily available carbohydrates.
Total N higher in faeces than in control soils	Increase in total N in faeces (Edwards et al., 1977) Increase in NH_4^+ and NO_3^- in faeces (Parle, 1963b)	Increased availability of nitrogen
Increase in exchangeable cations in faeces over controls	Increase in available cations in faeces(De Vleeschauwer et al., 1981; Teotia et al., 1950),	Excrement is rich in vitamins and minerals
% moisture content(A.D.basis) higher in faeces than controls	Increase in water holding capacity in faeces(Van Rhee, 1969b)	Excrement has high moisture content and ability to retain water
Generally pH of faeces around 6.5		pH of excrement around 6.5
	ingested litter fragmented after passage through gut(Bal, 1982)	structure of faeces results from mastication of ingesta

*reference
Lodha, 1974

Table 14:Relation of earthworm faecal microbiology to rumen faecal microbiology

Data and Observations from this Study	Evidence in the Literature	*Relation to Ruminant Faecal Microbiology
Higher numbers of actinomycetes, fungi and bacteria in faeces compared to control soils	Higher number of actinomycetes, fungi and bacteria in faeces compared to control soils (Atlavinyte et al.,1969-1980)	Increase in numbers of actinomycetes, fungi and bacteria in faeces
Higher numbers of *Cytophaga* sp. in faeces		*Cytophaga* sp. and aerobic cellulolytic bacteria closely related to rumen microflora associated with faeces
Generally fungi(including yeasts) present in higher numbers in faeces of earthworms	Number of fungi higher in faeces than control soils(Parle,1963a) Number of filamentous fungi and yeast higher in faeces than control soils.(Parle,1963a)	Fungal proliferation favoured in faeces
Filamentous fungi possessing dark fruiting bodies present in faeces of some earthworms where they were not present in the controls.		Fungi producing pigmented spores favoured
	Fungal spores demonstrated to survive passage through the earthworms gut. *L. terrestris* instrumental to the spread of fungal spores(Hutchison et al.,1956)	Fungi adapted to dung dependent on the prolific spore production which suvive passage through the gut
Proliferation of filamentous fungi in tunnels of *L. terrestris*	*L.terrestris*preferentially feeds on fungi(Cook et al.,1980) Reduced numbers of earthworms where fungicides used. (Cook et al.,1975;Niklas,1981)	Continuation of specialized fungi dependent on increased probability of ingestion of spore

*reference
Lodha,1974

of earthworms and ruminant digestion. Anomolies exist which suggest that depending on the species of earthworm involved one of the two processes dominates. This, in turn, most likely reflects the ecology of the different species of earthworms and ultimately their role in decomposition. *L. terrestris* appears to play a dominant role in affecting fungal activity while the geophages play a dominant role in anaerobic processes.

It was shown by Cook et al.(1980) that *L. terrestris* preferentially feeds on fungi. Cook et al.(1975) found that when fungicides were used in apple orchards to control disease, litter removal by *L. terrestris* was reduced. They concluded the influence of the fungicide was independent of any direct effect on the earthworms and suggested that it was due to fungicides interferring with the activity of leaf decomposing fungi and bacteria. Niklas(1981) came to a similar conclusion in a study involving *L. terrestris* and fungicides. He stated that "destruction of bark inhabiting fungi is not only an incidental side effect of bark removal" and that "individuals of *L. terrestris* were observed intentionally eating the fungi". It is known that species in other groups of soil fauna are fungivores(Twinn,1974;Harding et al.,1974;Edwards,1974) and it is not unrealistic to expect a similar phenomenon exists amongst earthworms. It is also of interest that *Cytophaga* sp. isolate from the faecal material of *L. terrestris* demonstrated considerable lytic activity against chitin(Table 15). Similarly, Parle(1963a)

Table 15:Assays for lytic capability of *Cytophaga* sp. isolates from the faecal material of *L. terrestris*

	Media Used in Assays for Lytic Activity(incubation period)					
Isolate Number	casein (3 days)	mannan (10 days)	cellulose (2 months)	fungal agar (14 days)	chitin suspension (10 days)	hydrolyzed chitin (14 days)
1	++	-	+	+	+	-
2	++	-	+	-	+	-
3	++	+		-	-	+
4	++	-	-	-	-	-
5	+	-		+	+	+
6	+	-		-	-	+
7	+	+	+	-	-	+
8	++	+		+	+	-
9	++	-		+	+	-
10	++	-	++	++	++	+
11	++	+	-	+	+	-
12	++	+	+	+	-	+
13	-	-	++	-	-	-
14	++	-		+	+	-
15	++	-		+	+	-
16	-	-	++			
17				-	-	-
18	-	++		-	-	-
19	-	-		+	-	+
20	++	-	++	-	+	-
21	++	+++	+	++	++	++

found chitinase activity was associated with the gut of *L. terrestris*. This suggests that a symbiosis may exist between the earthworm and microflora which permits digestion of the preferentially ingested fungi.

Other soil fauna which are fungivores feed predominantly on vegetative parts(hyphae,mycelium) (Richards,1974;Twinn,1974). Thus it would be advantageous for fungivores to propagate the growth of filamentous forms of fungi. In this study filamentous fungi were present in higher numbers in the faecal material of both groups of earthworms relative to the controls(Fig. 11), but the pigmented fruiting bodies such as those discussed by Lodha(1974) were associated only with *L. terrestris*(Fig. 11). Where non-filamentous fungi were present in the soil(Spruce Grove) their numbers were unaffected by the presence of earthworms(Fig. 11). In addition, yeasts were always present in high numbers in the faecal material of *L. terrestris* but were not detected in the controls or faecal material of *O.tyrtaeum/A.turgida*(Fig. 10). Parle(1963a) found that both yeasts and filamentous fungi were present in higher numbers in the faecal material of *L. terrestris* than in the control soil.

In most environments fungi constitute the primary decomposer population of plant materials(Eklund et al.,1974). *L. terrestris* is often said to play a primary role in decomposition by mixing litter into the soil and through fragmentation of the litter initiating the process of decomposition. It is proposed that the role of *L. terrestris* in decomposition be extended to include control over fungi which constitute the primary decomposer community. This will be discussed further in the context of the fate of organic matter(Section 4.3.4).

The geophages, on the other hand, appear to have a less dramatic influence on fungal populations. The presence of fruiting bodies associated with filamentous forms of fungi and high numbers of yeasts observed in the faecal material of *L. terrestris* were not found in the faecal material of *O.tyrtaeum/A.turgida* (Fig. 10,11). The higher number of filamentous fungi in the faecal material of the geophages in the Ellerslie soil relative to that determined in the faecal material of *L. terrestris* may be indicative of less specific fungal feeding by *O.tyrtaeum/A.turgida*(Fig. 11).

The different influence of the two groups of earthworms on the primary decomposers is most likely related to their feeding habits. *L. terrestris* actively collects and pulls litter beneath the soil surface and therefore would have greater access to fungi inhabiting the litter. Conversely the geophages have little direct contact with the litter since they are active predominantly in the mineral soil. In this case fungal decomposition in the litter would not be interfered with and could proceed normally.

Unlike *L. terrestris* the geophages have a consistant effect on the number of anaerobes found in their faecal material. In the case of *O.tyrtaeum/A.turgida* the level of enrichment of anaerobes in the faecal material is the same(Fig. 10) regardless of soil type and inherent numbers in the controls. In the Spruce Grove soil no anaerobes were detected in the control soil and still the level of enrichment in the faecal material is as high as in the other soils. *L. terrestris*, on the other hand, was only able to enrich anaerobes to the level of the geophages where anaerobes were detected in the control soil(CL,E-Fig. 10). These data suggest that the geophages are much more effective than *L. terrestris* in enhancing the population of anaerobes. The fact that the geophages were able to greatly enhance the number of anaerobes where they were not detected in the control suggests that the anaerobes may be a gut flora which were inoculated into the soil by the geophages.

Bal(1982) stated that geophages play an important role in the final stages of decomposition since their activity, dominantly in the mineral soil, leads to homogenization, mineralization and humification of organic matter. It is suggested in this thesis that the role of geophages in the final stages of decomposition is related to their strong influence on anaerobes and therefore decomposition through fermentation which leads to the complete breakdown of organic substrates. Further, it is of interest to note that pH values for the Spruce Grove soil in whih the geophages were active alone are significantly lower than those of the controls(Table 19). Also pH values for the leachates from the Spruce Grove and Ellerslie columns are significantly lower where the geophages were active alone when compared to the other four treatments(Appendix VIII). This may be a result of organic acids released through fermentative decomposition of organic substrates in the presence of geophages.

4.3.4 Fate of Organic Matter

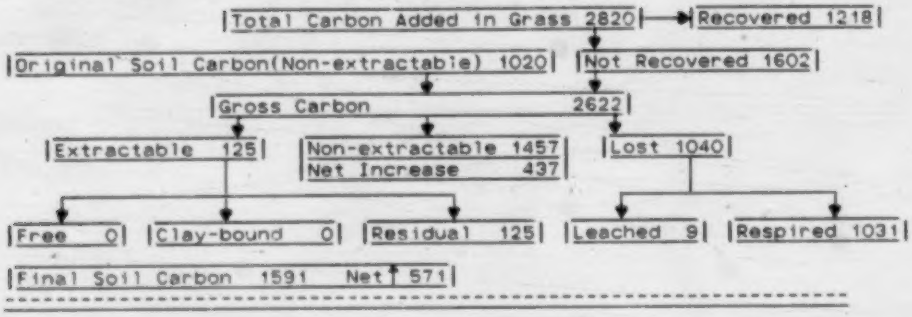
In this study the species of earthworm and type of soil were major factors determining the fate of organic matter in the soil. Earthworms regulated the fate of organic matter through their feeding habits and influence on the microbial community(see Sections 4.3.2, 4.3.3). Although distinctly different fates of organic matter exist between the different soils within similar treatments it is unclear what soil properties were responsible for these differences. Inherent organic carbon content, quantity of smectite clay and the inherent nature of the microbial community are properties which are implicated as being important in this regard. Their potential role in influencing the fate of organic matter will be discussed in the following sections according to Treatment. Models were prepared to represent the fate of carbon by Treatment for each soil type(Fig. 12-15). Numerical values for each component represent carbon in milligrams calculated on a mass basis. Calculations for each component are found in Appendix VII.

4.3.4.1 Control(Treatment 1)(Fig. 12)

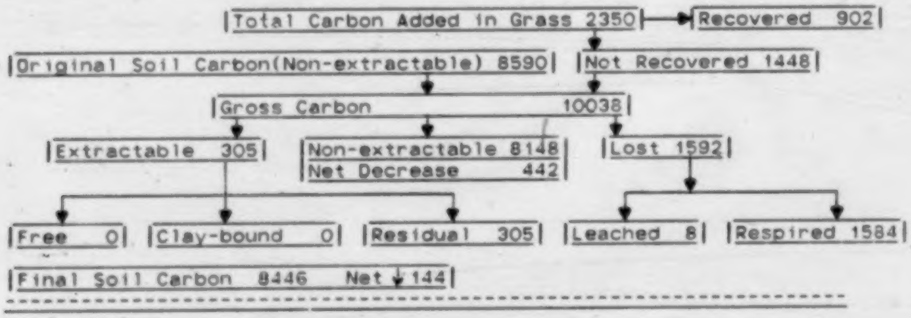
The models presented for Treatment 1(Fig.12) demonstrate the fate of organic carbon in the absence of earthworms. The addition of a new source of carbon(grass) to the soils resulted in a net increase in soil carbon in the Spruce Grove and Ellerslie soils, while a small net decrease in soil carbon occurred in the Cooking Lake soil.

Indications are that conditions in the Cooking Lake soil are more condusive to decomposition than in the Spruce Grove and Ellerslie soils. The value for carbon lost through respiration is much higher in the Cooking Lake soil than that for the other two soils. One reason for this may be the inherently higher amount of carbon in the Cooking Lake soil which could be supporting a microbial community that is more active than in the other soils and therefore able to take advantage of the new additions of carbon. Although the high values for total carbon in the Cooking Lake soil can partially be attributed to coal flecks some must also be attributed to organic sources of carbon which can be utilized by microorganisms. The facts that total organic carbon declined and the value for loss of carbon through respiration is higher than carbon not recovered from the grass, both indicate that carbon already present in the soil was decomposed.

SPRUCE GROVE


Total Carbon Added in Grass 2820
Recovered 1218
Original Soil Carbon(Non-extractable) 1020
Not Recovered 1602
Gross Carbon 2622
Extractable 125
Non-extractable 1457
Net Increase 437
Lost 1040
Free 0
Clay-bound 0
Residual 125
Leached 9
Respired 1031
Final Soil Carbon 1591 Net ↑ 571

COOKING LAKE


Total Carbon Added in Grass 2350
Recovered 902
Original Soil Carbon(Non-extractable) 8590
Not Recovered 1448
Gross Carbon 10038
Extractable 305
Non-extractable 8148
Net Decrease 442
Lost 1592
Free 0
Clay-bound 0
Residual 305
Leached 8
Respired 1584
Final Soil Carbon 8446 Net ↓ 144

ELLERSLIE

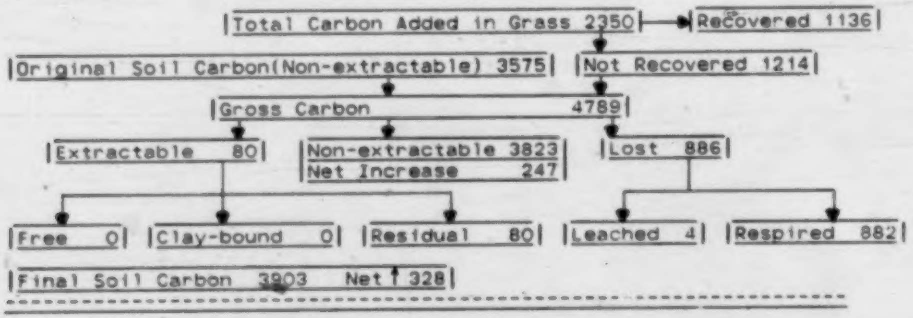

Total Carbon Added in Grass 2350
Recovered 1136
Original Soil Carbon(Non-extractable) 3575
Not Recovered 1214
Gross Carbon 4789
Extractable 80
Non-extractable 3823
Net Increase 247
Lost 886
Free 0
Clay-bound 0
Residual 80
Leached 4
Respired 882
Final Soil Carbon 3903 Net ↑ 328

Figure 12:Carbon balance for the controls(Treatment 1)
(carbon in total mg.-calculated on mass basis)

A scenerio different from that which exists for the Cooking Lake soil was found for the Spruce Grove and Ellerslie soils. Unlike the Cooking Lake soil a significant net increase in soil carbon resulted from the addition of carbon(grass) to the Spruce Grove and Ellerslie soils. The fact that losses of carbon through respiration in these two soils are lower than that for the Cooking Lake soil as well as being lower than values for carbon not recovered from the grass indicates that decomposition does not proceed as rapidly in the Spruce Grove and Ellerslie soils. In addition much of the increase in net soil carbon in these two soils can be attributed to the increase in the non-extractable component. This component most likely consists of resistant and non-decomposed organic materials (such as fragments of litter washed down into the soil) since the extraction procedure used would not recover such materials.

When comparing Ellerslie to the Spruce Grove soil, the former has a greater potential for favouring decomposition. Although the absolute value for carbon respired is lower in the Ellerslie soil, when it is taken as a percentage of carbon not recovered from the grass, it is clear that more of the added carbon was respired in the Ellerslie soil(73%) than in the Spruce Grove soil(64%). When data for the increase in non-extractable carbon are treated similarly the percentage values are 20% and 27% for the Ellerslie and Spruce Grove soils respectively. Therefore, of the carbon added, relatively more was respired and less added to the non-extractable component in the Ellerslie compared to Spruce Grove soil. Values arrived at in a similar fashion for the Cooking Lake soil where decomposition is highly favoured are 30% for net increase in the non-extractable component and >100% for respiration. The latter value exceeds 100% since carbon already present in the soil was decomposed.

Thus a sequence is established for conditions favourable to decomposition according to soil type. Conditions in the Cooking Lake soil highly favour decomposition, followed by the Ellerslie soil and lastly the Spruce Grove soil where conditions are least favourable to decomposition. This trend is also reflected in the difference among the C:N ratio of the soils where no grass was added(Treatment 5) and grass was added(Treatment 1)(Table 16). In the Cooking Lake soil the C:N ratio is 7.2 units lower in Treatment 1 than in Treatment 5. In the Ellerslie soil it is 1.3 units lower in Treatment 1, while in the Spruce Grove soil which least favours decomposition the C:N ratio is 3.4 units higher in Treatment 1 than in Treatment 5.

All three soil types are very similar in respect to the distribution of extractable carbon(determined as glucose equivalents) in that all of the extractable

Table 16:C:N ratios of parts according to soil type and treatment.

		Soil Type		
Treatment	Part	Spruce Grove	Cooking* Lake	Ellerslie
5	unaltered soil	6.2	24.9	12.2
1	unaltered soil	9.6	17.5	10.9
2	unaltered soil	10.8	19.6	10.2
	tunnel linings	8.6	16.8	10.4
	faecal pellets	9.1	15.0	10.8
3	unaltered soil	9.2	22.6	11.3
	tunnel linings	9.8	20.5	11.6
	faecal pellets	15.8	17.9	11.3
4	unaltered soil	8.2	24.2	9.6
	tunnel linings	11.4	20.1	10.0
	faecal pellets	13.9	15.2	10.2

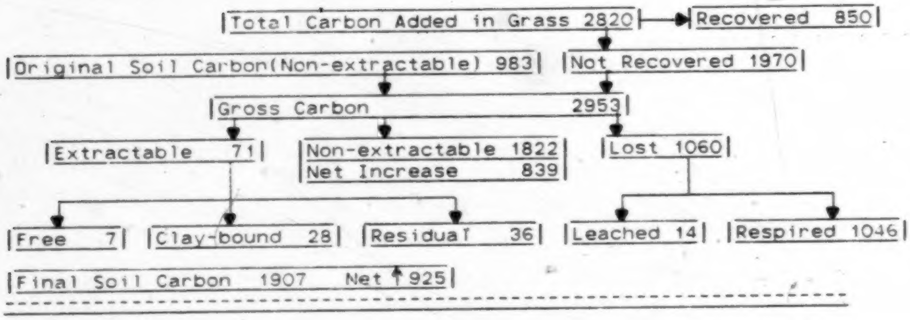
*C:N ratio's for this soil appear unusually high due to the presence of coal flecks in the soil carbon is in the residual component and none in the free or clay-bound components. The value for the Cooking Lake soil is higher than those for the Spruce Grove and Ellerslie soils. This probably reflects contributions to the residual component from carbon already present in the Cooking Lake soil.

4.3.4.2 *Octolasion tyrtaeum* and *Aporrectodea turgida*(Treatment 2)(Fig.13)

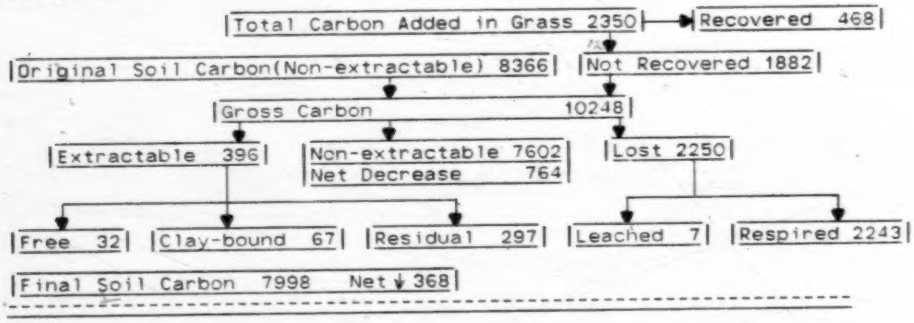
The presence of geophages increased the disparagy between trends for carbon balances in the three soils discussed for Treatment 1(Fig. 12). In all three soils less carbon was recovered from the grass than in Treatment 1. The additional carbon not recovered was greatest for the Ellerslie soil(512 mg) followed by Cooking Lake(434 mg) and Spruce Grove(368 mg) soils. Although additional carbon was not recovered for all three soils higher respiration losses were reflected only in the Cooking Lake and Ellerslie soils.

In the Spruce Grove soil the value for carbon lost to respiration remained about the same as in Treatment 1. The majority of carbon increase in the soil is in the non-extractable component, while the amount of carbon in the extractable component is slightly lower than in Treatment 1. These data indicate that although more carbon was added to the Spruce Grove soil in the presence of the geophages, this did not have an accelerating influence on decomposition. The C:N ratio

SPRUCE GROVE


Total Carbon Added in Grass 2820
Recovered 850
Original Soil Carbon(Non-extractable) 983
Not Recovered 1970
Gross Carbon 2953
Extractable 71
Non-extractable 1822
Net Increase 839
Lost 1060
Free 7
Clay-bound 28
Residual 36
Leached 14
Respired 1046
Final Soil Carbon 1907 Net ↑ 925

COOKING LAKE


Total Carbon Added in Grass 2350
Recovered 468
Original Soil Carbon(Non-extractable) 8366
Not Recovered 1882
Gross Carbon 10248
Extractable 396
Non-extractable 7602
Net Decrease 764
Lost 2250
Free 32
Clay-bound 67
Residual 297
Leached 7
Respired 2243
Final Soil Carbon 7998 Net ↓ 368

ELLERSLIE

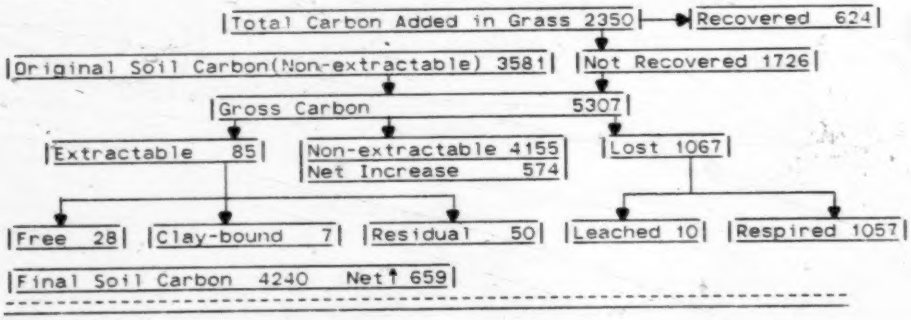

Total Carbon Added in Grass 2350
Recovered 624
Original Soil Carbon(Non-extractable) 3581
Not Recovered 1726
Gross Carbon 5307
Extractable 85
Non-extractable 4155
Net Increase 574
Lost 1067
Free 28
Clay-bound 7
Residual 50
Leached 10
Respired 1057
Final Soil Carbon 4240 Net ↑ 659

Figure 13: Carbon balance for soils in the presence of *O. tyrtaeum* and *A. turgida*(Treatment 2) (carbon in total mg.-calculated on mass basis)

of the unaltered soil in Treatment 2 is higher than that for the soil in Treatment 1(Table 16). Even though the C:N ratios of material which passed through the gut of the earthworm(faecal pellets,tunnel linings) are lower than that of the soil part they are not reduced much beyond the C:N ratio of the soil in Treatment 1(Table 16).

A major difference between Treatment 2 and Treatment 1 for the Spruce Grove soil exists in the nature of the extractable carbon. Although the total amount extracted is slightly lower than for Treatment 1 some of the carbon is present in the clay-bound and free components.

Thus some net benefits to the Spruce Grove soil were brought about by the presence of the geophages. More organic carbon was introduced to the soil than in Treatment 1. The C:N ratio of material ingested by the earthworms was lowered to a similar level which existed in Treatment 1. Some carbon was stabilized through binding with clays which was not evident in Treatment 1.

Carbon accumulated in Treatment 2 of the Ellerslie soil in a similar fashion to the Spruce Grove soil but decomposition is favoured slightly more in this soil. Although carbon lost to respiration in the Ellerslie soil is about the same as for the Spruce Grove soil(Fig. 13) this represents a higher loss relative to Treatment 1 for the Ellerslie soil(Fig. 12). The majority of carbon added to the Ellerslie soil is present in the non-extractable component(Fig. 13) but the C:N ratio of the unaltered soil is maintained at a significantly lower level than in Treatment 5 and at a slightly lower level than in Treatment 1(Table 16). These data indicate that the presence of geophages in the Ellerslie soil resulted in similar accumulations of carbon when compared to the Spruce Grove soil and also suggests that decomposition was accelerated over that which occurred in the absence of geophages(Treatment 1).

The difference in the nature of extractable carbon evident in the Spruce Grove soil was also evident in the Ellerslie soil. Although similar amounts of carbon were extracted from the soil where geophages were and were not present clay-bound and free components of carbon were found only in the presence of the geophages. More clay-bound carbon was extracted from the Spruce Grove soil(Treatment 2) than the Ellerslie soil. This may reflect the fact that geophages ingested a larger volume of soil in the Spruce Grove soil than in the Ellerslie soil(Table 17) thus increasing the probability for contact between organic and inorganic soil constituents.

The response of the carbon balance for Treatment 2 in the Cooking Lake soil was very different from that of the other two soils but followed the trend established in Treatment 1. Although more carbon was not recovered from the grass in Treatment 2 than Treatment 1 there was

Table 17:Volume(cm^3) of soil ingested by earthworms.

	Treatment Number		
Soil Type	2	3	4
Spruce Grove	101	157	222
Cooking Lake	74	157	335
Ellerslie	53	50	113

a higher loss of carbon through respiration. The fact that carbon lost through respiration(Treatment 2) exceeded the value for carbon not recovered from the grass and that carbon in the non-extractable component decreased significantly supports the earlier statement that not only carbon from the grass was decomposed but also carbon alreadly present in the soil was lost. The collective result of this increased biological activity was a net drop in total soil carbon. The C:N ratios of parts in Treatments 1 and 2 for the Cooking Lake soil exhibit the same trend as the Spruce Grove soil(Table 16). The C:N ratio for the unaltered soil material in Treatment 2 is higher than that for Treatment 1 while those for soil which was ingested by the earthworms are lower. The major difference lies in the fact that all of the C:N ratio's for Treatments 1 and 2 are significantly lower than that for Treatment 5 for the Cooking Lake soil while they are all higher than Treatment 5 for the Spruce Grove soil(Table 16).

The fate of extractable carbon in the Cooking Lake soil was similar to that of the other two soils. Approximately the same amount of carbon was extracted from the soil in Treatment 2 as in Treatment 1 but carbon was present in the clay-bound and free components in Treatment 2.

In general all three soil types benefitted by the presence of the geophages. In all cases the absolute amount of carbon extracted from the same soils where geophages were present(Treatment 2) and absent(Treatment 1) showed little difference but there were differences in the nature of the extracted carbon. There was carbon extracted in the free and clay-bound component where the geophages were present whereas no carbon was found in these components in their absence.

In this study the clay-bound component is of great interest since it is important to stabilization of soil organic matter and soil structure. In this regard the Cooking Lake soil appeared to receive the greatest net benefit in terms of the absolute amount of clay-bound carbon extracted. This benefit is somewhat devalued when the efficiency of the carbon balance is examined. The high loss of carbon through respiration in the Cooking Lake soil relative to the others resulted in a loss of carbon to the system which would never be recovered. Although the absolute amount of carbon in the clay-bound component is highest for the Cooking Lake soil it represents a relatively small(17%) proportion of the carbon extracted indicating a low efficiency for stabilization of carbon.

The Spruce Grove soil, on the other hand, received a smaller net benefit in terms of the absolute amount of carbon stabilized but was more efficient in terms of the carbon balance. Respiration losses were no higher than in the control(Treatment 1) and a high proportion of the extractable carbon was stabilized(36%). The total carbon in the Spruce Grove soil increased significantly. Although this carbon exists mainly in the non-extractable component at it was retained in the soil and could be available over the long term for future stabilization.

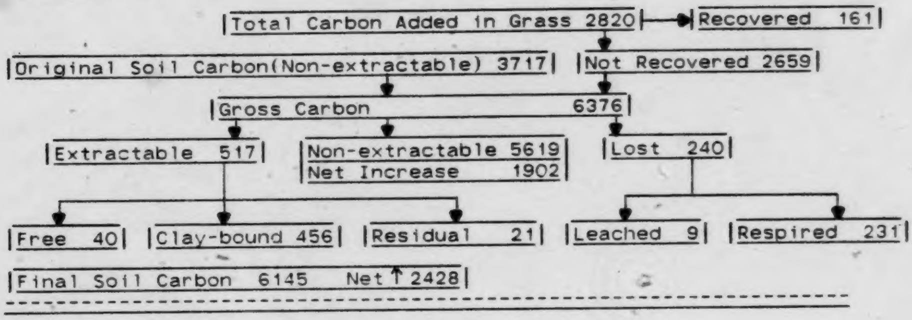
The Ellerslie soil appeared to benefit the least of the three soils by the presence of the geophages. Loss of carbon to respiration was slightly higher than in the control(Treatment 1) and the proportion of carbon extracted in the clay-bound component was the lowest for all three soils(7%). However, the net increase in total soil carbon can be viewed as a benefit since it was retained in the soil and would be available for future utilization.

4.3.4.3 *L.terrestris*(Treatment 3)(Fig.14)

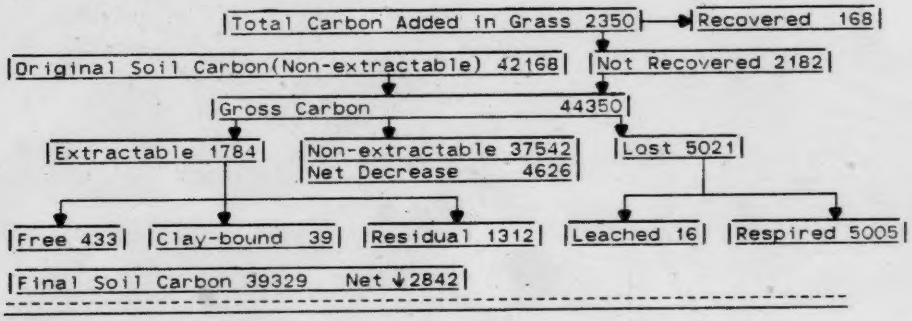
The different trends established for the carbon balance between the soils in Treatment 1 and accentuated by the presence of the geophages are very strongly expressed in the presence of *L. terrestris*. This is attributed to the feeding habit of *L. terrestris*. Grass added to the columns was pulled beneath the soil surface;*L. terrestris* interacted with primary decomposers(mainly fungi-Section 4.3.3); and a larger volume of soil was ingested by *L. terrestris* than the geophages(Table 17). The majority of carbon added as grass was not recovered in all three soils reflecting the feeding habit of *L. terrestris*. Although no significant difference existed in the amount of grass not recovered between the different soils, distinctly different patterns for the carbon balance resulted form the interaction of *L. terrestris* with soil type.

In the presence of *L. terrestris* the carbon balance in the Spruce Grove soil was highly efficient in stabilization of organic matter. Loss of carbon due to respiration was reduced by nearly 80% relative to Treatments 1 and 2. Significantly more carbon was extracted from this treatment than any other for the Spruce Grove soil and of this carbon 88% is present in the clay-bound component. The net increase in soil carbon is more than double that of Treatment 2. Although the majority of this carbon is in the non-extractable

SPRUCE GROVE


Total Carbon Added in Grass 2820
Recovered 161
Original Soil Carbon(Non-extractable) 3717
Not Recovered 2659
Gross Carbon 6376
Extractable 517
Non-extractable 5619
Net Increase 1902
Lost 240
Free 40
Clay-bound 456
Residual 21
Leached 9
Respired 231
Final Soil Carbon 6145 Net ↑ 2428

COOKING LAKE


Total Carbon Added in Grass 2350
Recovered 168
Original Soil Carbon(Non-extractable) 42168
Not Recovered 2182
Gross Carbon 44350
Extractable 1784
Non-extractable 37542
Net Decrease 4626
Lost 5021
Free 433
Clay-bound 39
Residual 1312
Leached 16
Respired 5005
Final Soil Carbon 39329 Net ↓ 2842

ELLERSLIE

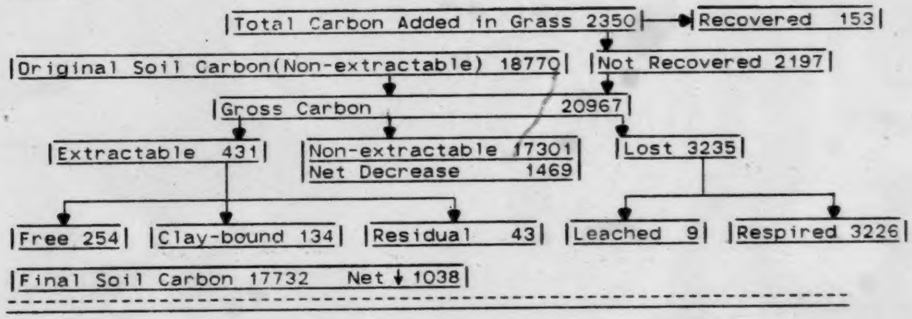

Total Carbon Added in Grass 2350
Recovered 153
Original Soil Carbon(Non-extractable) 18770
Not Recovered 2197
Gross Carbon 20967
Extractable 431
Non-extractable 17301
Net Decrease 1469
Lost 3235
Free 254
Clay-bound 134
Residual 43
Leached 9
Respired 3226
Final Soil Carbon 17732 Net ↓ 1038

Figure 14: Carbon balance for soils in the presence of *L. terrestris*(Treatment 3) (carbon in total mg.-calculated on mass basis)

component it is retained in the soil and would be available for future utilization. The higher C:N ratios(Table 16-faecal pellets), lower loss of carbon due to respiration, and greater increase in total carbon relative to Treatment 1 and 2 indicate that decomposition was retarded in the Spruce Grove soil in the presence of *L. terrestris*. This may be attributed to the control *L. terrestris* has over the primary decomposers(especially fungi) as discussed in Section 4.3.3. The retardation of decomposition when *L. terrestris* was present to bring inorganic and organic constituents into intimate contact proved highly beneficial to the Spruce Grove soil. The absolute quantity of extractable carbon was highest for the Spruce Grove soil in this treatment and the majority of this carbon was present in the clay-bound component and therefore stabilized.

The Cooking Lake soil responded very differently to the presence of *L. terrestris*. The loss of carbon to respiration was considerably higher than that from the Spruce Grove soil(Fig. 14) resulting in a significant drop in total soil carbon. Although the total extractable carbon was highest for this particular soil and treatment only a small proportion(2%) of it is in the clay-bound component. Thus, the presence of *L. terrestris* in the Cooking Lake soil led to greater decomposition than in the other treatments(higher respiration, greater drop in total carbon) but little net benefit to the soil since a very small quantity of the extractable carbon was stabilized.

The Ellerslie soil responded entirely different from the other two soils to the presence of *L. terrestris*. Decomposition was enhanced over that which occurred in Treatments 1 and 2 although not as dramatically as the increase in the Cooking Lake soil. Carbon lost to respiration was higher for the Ellerslie soil in the presence of *L. terrestris* than in Treatments 1 or 2 but not as high as that observed for the Cooking Lake soil. The first decrease for total carbon was observed in the Ellerslie soil but again this decrease is not as great as that in the Cooking Lake soil.

The enhanced decomposition in the presence of *L. terrestris* in the Cooking Lake and Ellerslie soils but not the Spruce Grove soil may be due to interactions with the decomposer organisms. In the Cooking Lake and Ellerslie soils *L. terrestris* was able to enrich the soil with anaerobes(Fig. 10) and maintain viable fungal decomposers(as described by Lodha(1974) and discussed in Section 4.3.3) while they were not able to do so in the Spruce Grove soil. Assays for acetylene reduction by *Spirillum* enriched in the tunnel linings of *L. terrestris* indicated that ethylene production by these bacteria is much higher in the Cooking Lake than Ellerslie or Spruce Grove soils(Appendix IX).

Contribution to soil nitrogen by nitogen-fixing *Spirillum* enriched in the presence of *L. terrestris* may be important to the accelerated decomposition observed for the Cooking Lake soil.

This accelerated decomposition proved more beneficial to the Ellerslie soil than the Cooking Lake soil. Total carbon did not decrease as much in the Ellerslie soil while a higher proportion(31%) of the extractable carbon is present in the clay-bound component of the Ellerslie soil as compared to Cooking Lake(2%). The fact more carbon was stabilized in the Ellerslie soil than the Cooking Lake soil may result from the presence of a higher percentage of smectite clay(Table 18) which would be more active in binding with organic constituents than other clay types present in these soils.

Table 18: Percent of smectite clay present in the parent materials of the Spruce Grove, Cooking Lake and Ellerslie soils.

Soil Type	%clay	% of clay smectite*	% of soil smectite
Spruce Grove	5	60	3.0
Cooking Lake	35	33	11.5
Ellerslie	33	60	19.8

*references

Spruce Grove - Pawluk et al.(1982)
Cooking Lake - Abder-Ruhman(1980)
Ellerslie - Sandbourn(1981)

4.3.4.4 *Octolasion tyrtaeum*,*Aporrectodea turgida*,*Lumbricus terrestris*(Treatment 4)(Fig.15)

Benefits accrued to the Spruce Grove soil from *L. terrestris* acting alone were lost when the geophages were permitted to co-exist with *L. terrestris*. In fact net benefits to the soil in terms of stabilized organic matter are less than where either ecological group was active in the soil alone. Loss of carbon to respiration is significantly higher than that in Treatment 3 but remained lower than that in the control or where only geophages were active. Total extractable carbon is the lowest for any of the treatments in the Spruce Grove soil and a very small quantity of this is present in the clay-bound component. Total soil carbon increased by an amount similar to that in Treatment 3 but the majority of this is present in the non-extractable component. Thus net benefits that accrued to the Spruce Grove soil in the presence of both ecological groups of earthworms were minimal. A negligable amount of carbon was stabilized and the majority of carbon introduced to the soil through the withdrawal of grass by *L. terrestris* likely remained in a relatively undecomposed state as part of the non-extractable component.

Loss of carbon through respiration was lower for both the Cooking Lake and Ellerslie soils where both ecological groups were present, but higher where the geophages were active alone when compared to Treatment

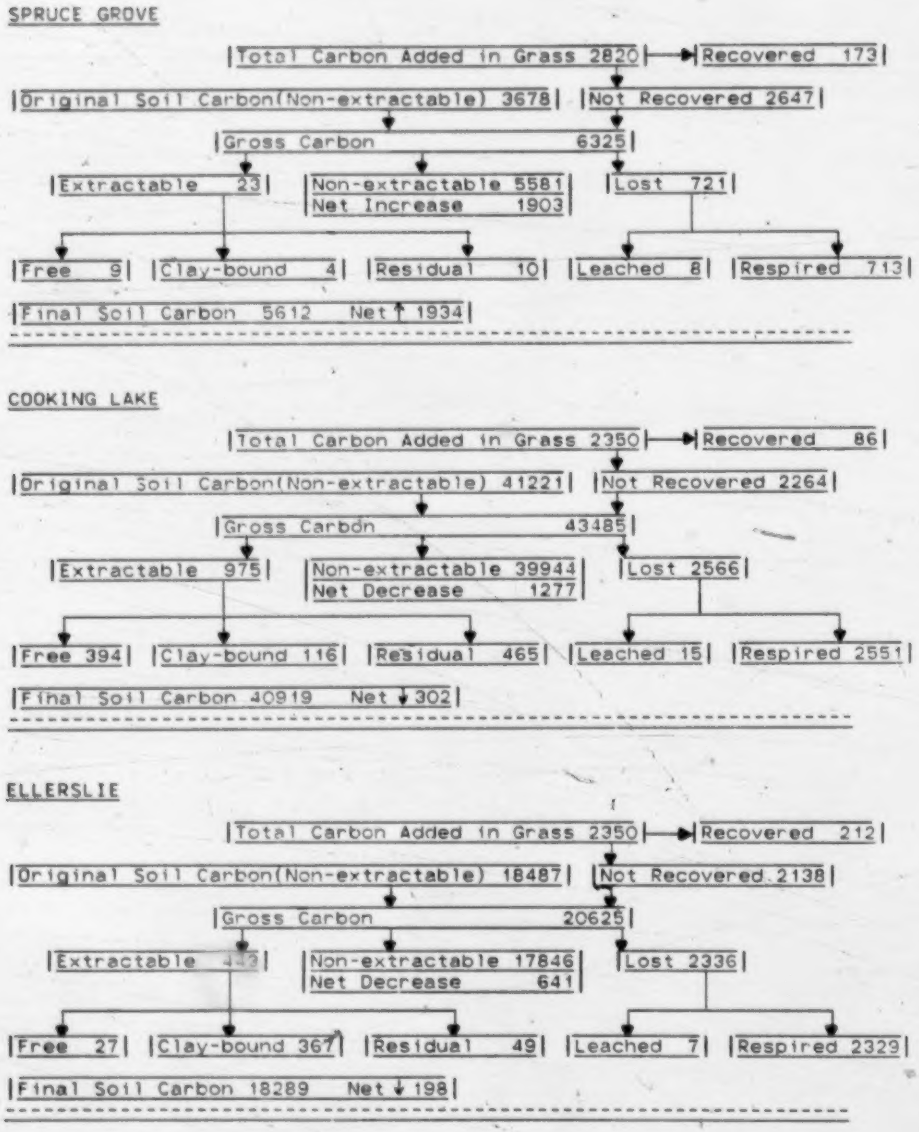

SPRUCE GROVE
Total Carbon Added in Grass 2820
Recovered 173
Original Soil Carbon(Non-extractable) 3678
Not Recovered 2647
Gross Carbon 6325
Extractable 23
Non-extractable 5581
Net Increase 1903
Lost 721
Free 9
Clay-bound 4
Residual 10
Leached 8
Respired 713
Final Soil Carbon 5612 Net ↑ 1934
COOKING LAKE
Total Carbon Added in Grass 2350
Recovered 86
Original Soil Carbon(Non-extractable) 41221
Not Recovered 2264
Gross Carbon 43485
Extractable 975
Non-extractable 39944
Net Decrease 1277
Lost 2566
Free 394
Clay-bound 116
Residual 465
Leached 15
Respired 2551
Final Soil Carbon 40919 Net ↓ 302
ELLERSLIE
Total Carbon Added in Grass 2350
Recovered 212
Original Soil Carbon(Non-extractable) 18487
Not Recovered 2138
Gross Carbon 20625
Extractable 443
Non-extractable 17846
Net Decrease 641
Lost 2336
Free 27
Clay-bound 367
Residual 49
Leached 7
Respired 2329
Final Soil Carbon 18289 Net ↓ 198

Figure 15: Carbon balance for soils in the presence of *O. tyrtaeum*, *A. turgida* and *L. terrestris*(Treatment 4). (carbon in total mg.-calculated on mass basis)

3. This resulted in a net decrease in total carbon for both soils although the decrease is small in the Cooking Lake soil and likely insignificant in the Ellerslie soil. Both soils benefitted in terms of stabilized organic matter where both ecological groups were present, but the benefits to the Ellerslie soil by far exceeded those to the Cooking Lake soil. The absolute amount(367 mg) and proportion of the extractable carbon(83%) in the clay-bound component in the Ellerslie soil was far greater than similar values for the Cooking Lake soil(116 mg,18% respectively). Although similar scenarios existed in the two soils in regards to carbon not recovered from the grass, loss of carbon through respiration and decline in total soil carbon, more extractable carbon was stabilized in the Ellerslie soil. This may be attributed to the difference between the soils in regards to the quantity of smectite clays present which is much higher in the Ellerslie than Cooking Lake soil(Table 18).

4.3.5 Summary

The traditional viewpoint regarding earthworms and decomposition is that earthworms ingest and mix litter into the soil and by doing so increase the availability of substrates to microorganisms which in turn increase in number so that decomposition proceeds more rapidly than where earthworms are absent. Data presented here indicates that such a viewpoint is too simplistic and that a variety of factors must be taken into consideration when evaluating earthworms and their role in decomposition. Some of these factors include the species of earthworm and how it functions ecologically, how it feeds and interacts with decomposer organisms and the nature of the soil inwhich it exists. In this study where two ecological groups of earthworms, alone and in conjunction, were active in three different soil types, wide ranging responses in terms of carbon balance occurred. These responses were linked to the aforementioned factors although other factors, as yet not considered, are probably important as well.

All three soils benefitted to some degree in regards to stabilization of organic matter when earthworms were present. In every case where earthworms were present some of the extractable carbon was present in the clay-bound component while in all of the controls(Treatment 1) carbon was absent in the clay-bound component.

In this study the sandy loam textured soil(Spruce Grove) benefitted the most when *L. terrestris* was active in the soil alone. The absolute amount(456 mg) and proportion(88%) of extractable carbon in the clay-bound component for this soil was higher than for any other treatment while losses of carbon to respiration were lowest(231 mg). Retarded decomposition which may have been brought about by the control of decomposer organisms(fungi,anaerobes) by *L. terrestris* favoured stabilization of organic matter in the Spruce Grove soil. Where decomposition proceeded more rapidly(Treatments 1,2,4) less carbon was stabilized and more carbon was lost to respiration.

The Ellerslie soil(SiCL) benefitted the most when both ecological groups of earthworms were present(Treatment 4). The highest amount(367 mg) and proportion(83%) of stabilized carbon was present in this treatment while the loss of carbon to respiration was intermediate to those in Treatments 2 and 3. Decomposition was enhanced in the Ellerslie soil in the presence of both species of earthworms over that which occurred in the similar treatment for the Spruce Grove soil. The enhanced decomposition in the Ellerslie soil was attributed to the ability of the earthworms to propagate microorganisms. Unlike the Spruce Grove soil accelerated decomposition in the presence of both groups of earthworms led to greater stabilization of organic matter in the Ellerslie soil. This may result from the higher percentage of smectite clays present.

Although some extractable carbon was stabilized in each treatment where earthworms were present in the Cooking Lake soil the amounts and proportions were not as high as those achieved in the Spruce Grove soil-Treatment 3 and the Ellerslie soil-Treatment 4. Decomposition was enhanced by the presence of earthworms in all cases in the Cooking Lake soil as indicated by higher respiration losses of carbon and lower C:N ratios than in the control(Treatment 1). Although decomposition was enhanced in Treatment 4 of the Cooking Lake soil as was the case for Treatment 4 for the Ellerslie soil a much lower amount(116 mg) and proportion(18%) of extractable carbon was stabilized. This may reflect the lower percentage of smectite clays present in the Cooking Lake soil relative to the Ellerslie soil. When assessing the total benefit to the soil, indications are that the Cooking Lake soil benefitted the most where the geophages were active alone. Although more carbon was stabilized where both ecological groups were present this was also the treatment where extremely adverse structure was observed(Section 4.2.1).

4.4 Earthworms and Soil Chemistry

4.4.1 Introduction

Routine chemical analyses were performed on all parts(unaltered soil,tunnel linings and faecal pellets) dissected from the soil columns. These data are presented in Tables 19-21. In addition the grass recovered at the termination of the experiment from Treatments 1 and 2 was analyzed for the amount of Ca, Mg, Na and K present in order to determine their loss. These data are presented in Table 22. A similar analysis was not done on the grass recovered from Treatments 3 and 4 because of the small sample size available. Leachates were analyzed for the same elements as well as for the concentration of soluble inorganic carbon and pH(Appendix VIII). Collectively these data provide a basis for a cursory examination of the role of earthworms in cycling of Ca, Mg, Na and K. On account of the general nature of the analyses and the fact that this was a secondary objective of the study, the data will not be discussed in detail. Primarily, the data helped to indicate areas for potential further research. The nature of the analyses was not detailed enough to permit interpretation of the origin(organic vs. inorganic) of elements lost through leaching although some inferences can be drawn on the basis of the collective data.

4.4.2 Total Exchange Capacity(TEC)

The values for total exchange capacity for the unaltered soil from all treatments and soil types are not significantly different(Table 19). The total exchange capacity is significantly higher in the faecal pellets of earthworms than in the unaltered soil and tunnel linings in the Cooking Lake and Ellerslie soils(Table 20). The value for TEC in the faecal material from the Spruce Grove soil is also higher than the values for the tunnel linings and unaltered soil but the difference is not statistically significant. The amounts of extractable Ca(Ellerslie and Spruce Grove soils-Table 21) and exchangeable Mg and K(Table 20) are also highest in the faecal material.

The higher values for TEC in the faecal material of earthworms may result from the presence of high

Table 19:Chemical analyses for the unaltered soil from each treatment and soil type.

(values within rows not preceeded by similar letters are significantly different,P=.05)

		Treatment Number				
Analysis	Soil Type	1	2	3	4	5
Total Exchange Capacity (me/100 g)	No Interaction	a 17.90	a 17.07	a 17.48	a 17.10	a 18.82
Extractable Calcium (me/100 g)	Spruce Grove	b 7.30	a 5.90	ab 6.35	a 5.80	a 6.10
	Cooking Lake	a 26.95	b 30.30	cd 35.35	d 36.15	c 35.20
	Ellerslie	a 47.15	c 50.85	b 48.55	c 50.35	b 48.65
Exchangeable Magnesium (me/100 g)	Spruce Grove	a 1.55	a 1.85	a 1.85	a 1.80	a 1.75
	Cooking Lake	c 4.25	c 4.40	bc 4.00	ab 3.80	a 3.55
	Ellerslie	a 6.10	a 6.40	a 6.05	a 6.10	a 6.10
Exchangeable Sodium (me/100 g)	No Interaction	a .24	a .26	a .26	a .26	a .24
Exchangeable Potassium (me/100 g)	Spruce Grove	c .32	d .40	b .21	bc .24	a .08
	Cooking Lake	c .36	d .46	abc .27	ab .24	a .18
	Ellerslie	bc .44	c .49	ab .37	ab .35	a .33
pH	Spruce Grove	b 6.8	a 5.0	b 5.8	a 5.2	b 6.1
	Cooking Lake	a 7.5	a 7.6	a 7.6	a 7.8	a 7.8
	Ellerslie	a 7.7	a 7.8	a 7.8	a 7.8	a 7.8
Inorganic Carbon(%)	Treatment Only	a .51	ab .63	b .76	ab .73	ab .72
Organic Carbon(%)	No Interaction	a .67	a .67	a .60	a .63	a .64

Table 20:Chemical analyses of parts according to soil type.

(values within type of analysis not preceeded by similar letters are significantly different, P=.05)

Analysis	Soil Type	PART		
		Unaltered Soil	Tunnel Linings	Faecal Pellets
Total Exchange Capacity (me/100 g)	Spruce Grove	a 10.07	a 10.32	a 12.22
	Cooking Lake	b 19.58	b 21.47	c 31.95
	Ellerslie	b 22.00	b 23.40	c 33.10
*Extractable Calcium (me/100 g)				
Exchangeable Magnesium (me/100 g)	Spruce Grove	a 1.83	a 1.88	a 2.18
	Cooking Lake	b 4.07	c 4.32	c 5.38
	Ellerslie	d 6.18	e 6.35	e 7.08
*Exchangeable Sodium (me/100 g)				
Exchangeable Potassium (me/100 g)	Spruce Grove	a .28	a .32	b 1.07
	Cooking Lake	a .32	a .38	b 1.03
	Ellerslie	a .40	a .52	c 1.68
pH	Spruce Grove	a 5.3	a 5.4	a 5.2
	Cooking Lake	d 7.6	d 7.6	b 6.6
	Ellerslie	d 7.8	d 7.7	c 7.0
Inorganic Carbon(%)	Spruce Grove	a 0.00	a 0.00	a 0.02
	Cooking Lake	c 1.04	c 0.89	b 0.52
	Ellerslie	c 1.08	c 0.98	c 0.98
Organic Carbon(%)	Spruce Grove	a 0.19	b 0.36	e 1.00
	Cooking Lake	e 1.17	f 1.34	g 1.86
	Ellerslie	c 0.54	d 0.87	g 1.76

*See Table 21 for interaction with treatments

Table 21: Extractable Ca(me/100 g) and Exchangeable Na(me/100 g) in the unaltered soil and faecal pellets from the Spruce Grove, Cooking Lake and Ellerslie soils.

(values not preceeded by similar letters are significantly different, P=.05)

Element	Soil Type	Part	TREATMENT NUMBER 2	3	4
Calcium	Spruce Grove	Unaltered soil	a 5.9	a 6.4	a 5.8
		Faecal pellets	a 6.4	a 6.0	a 5.4
	Cooking Lake	Unaltered soil	c 30.3	c 35.4	c 36.2
		Faecal pellets	bc 25.0	bc 27.2	b 22.3
	Ellerslie	Unaltered soil	d 50.8	d 48.6	d 50.4
		Faecal pellets	d 64.4	d 45.9	d 37.0
Sodium	Spruce Grove	Unaltered soil	c .20	bc .19	abc .16
		Faecal pellets	abc .17	a .06	a .06
	Cooking Lake	Unaltered soil	abc .18	abc .16	abc .18
		Faecal pellets	ab .10	a .06	abc .14
	Ellerslie	Unaltered soil	e .42	e .42	e .44
		Faecal pellets	e .44	d .30	cd .24

Table 22:Percent Loss of elements from the grass added to the columns(Treatments 1 and 2) for all soil types.

Element	Treatment Number 1	Treatment Number 2	Significantly Different (P=.05)
Ca	4	32	*
Mg	43	64	*
Na	86	79	No Sig. Diff.
K	72	87	(1)

(1)Data provided for the Ellerslie soil only. No significant differences were found for the other two soil types.

concentrations of organic matter(% Organic Carbon-Table 20) as well as colloidal inorganic matter(observed in thin section). The fact that the significantly higher values for TEC occurred only in soils containing a high percentage of clays suggests that colloidal inorganic matter may be contributing significantly to the increase in total exchange capacity.

An attempt was made to quantify the content of colloidal inorganic matter in the faecal pellets and control soils but no consistant results were obtained. This, in part, was the result of the small sample size available for analysis.

4.4.3 Calcium

Interpretation of data for calcium is complicated by the fact that the parent materials were calcareous (dominantly dolomitic, calcium and magnesium carbonates) and that in Treatment 2 losses of calcium from the grass were significantly greater than losses from the control(Table 22). Thus, it is difficult to determine what proportions of Ca loss occurred through leaching from organic(grass) vs. inorganic(soil carbonates) sources.

Data presented in Table 21 indicate that extractable calcium is significantly lower in the faecal pellets than in the unaltered soil for the Cooking Lake soil. This likely reflects losses of $CaCO_3$ from the faecal material since both pH and inorganic carbon values are significantly lower in the faecal material(Table 20).

Data for pH and concentration of soluble inorganic carbon in the leachates(Appendix VIII) tend to indicate that reduction of pH is associated with an increased rate of carbonate release from soils where the geophages were active alone(Treatment 2). This trend is most strongly expressed in the Spruce Grove soil where inherent carbonate levels and clay buffering are both low. The concentration of inorganic carbon in the leachates is initially(2 months) high but this quickly drops to nil at the end of 11 months. This loss of inorganic carbon occurs concomitantly with a significant drop in pH. A similar trend exists in the Ellerslie leachates although it is not as strongly expressed. This is probably a reflection of the high inherent concentration of carbonates and the high clay buffering in the Ellerslie soil compared with the Spruce Grove soil.

Data for calcium concentrations in the leachates do not follow trends which can be interpreted as having an association with the release of soluble inorganic carbon alone. This likely reflects contributions to Ca in the leachates from the grass.

4.4.4 Magnesium

Data presented in Table 20 indicate the amount of exchangeable magnesium is significantly higher in the faecal pellets and tunnel linings than in the unaltered soil for the Cooking Lake and Ellerslie soils. This likely reflects contributions from the decomposed and leached grass. Although a small amount may be added from dissolved inorganic carbonates, more Mg was lost from the grass in the presence of the geophages(Treatment 2) than in the control(Treatment 1)(Table 22). Data for the concentration of Mg in the leachates(Appendix VIII) indicates that more Mg was lost from columns where grass was added(Treatments 1-4) than from where no grass was added(Treatment 5), regardless of the presence of earthworms.

In some cases more Mg was lost from columns where *L. terrestris* was present(Treatments 3 and 4). This most likely reflects the ecology of the earthworm. *L. terrestris* constructs permanent, vertically oriented channels which would enhance the leaching rate of mobile elements.

4.4.5 Sodium

The values for exchangeable sodium in the unaltered soil from all treatments and soil types are not significantly different(Table 19). At the interaction level between species of earthworm and soil type significant differences in the amount of exchangeable Na present occurred between the faecal pellets and unaltered soil(Table 21). In the Spruce Grove and Ellerslie soils the amount of exchangeable Na is significantly lower in the faecal material from Treatments 3 and 4(*L. terrestris* present) relative to the unaltered soil. Lower values for exchangeable Na in the faecal material may be related to the ecological behavior of *L. terrestris*. Faecal material was deposited on the soil surface in close proximity to the large, vertically oriented channel. When the columns were leached, ions with high mobility such as Na, could be preferentially leached from the surficially deposited casts, through the tunnel and out of the soil. High concentrations of Ca ions likely displaced Na ions on the exchange complex and released them into the leaching solution. In general the concentration of Na in the leachates(Appendix VIII) from Treatments 3 and 4 are higher than similar values from Treatments 1, 2 and 5.

In Treatment 2 for the Ellerslie and Cooking Lake soils no significant differences in the amount of exchangeable Na occurred between the unaltered soil and faecal material of the geophages(Table 21). The loss of Na from the added grass(Table 22) and through leaching(Appendix VIII) is not significantly different between Treatment 2 and the control. These data suggest that the net effect of the leaching environment created by the tunnelling of the geophages is not significantly different from the control. Although many channels are formed throughout the soil by the geophages they are ephemeral and discontinuous. *L. terrestris*, on the other hand, constructs a permanent, vertically oriented channel and this would enhance leaching and loss of mobile nutrient elements.

Indications are that Na lost through leaching in this study originated largely from the grass. High concentrations of Ca on the exchange complex likely prevented the retention of Na in the soil. Values for Na concentrations in the leachates are frequently higher in Treatment 1(control +grass) than Treatment 5(control -grass). The concentration of Na in the leachates is even higher in Treatments 3 and 4 than Treatment 1, where *L. terrestris* withdrew grass from the surface into their channels.

4.4.6 Potassium

Data presented in Table 19 indicate there are some significant differences in the amount of exchangeable K present in the unaltered soil from all treatments. Values for the control where grass was present(Treatment 1) are higher than for the control where grass was absent(Treatment 5). Exchangeable K values in the unaltered soil from

Treatments 3 and 4 are about the same as for the control where grass was present(Treatment 1). Where the geophages were present(Treatment 2) the values for exchangeable K are significantly higher in the unaltered soil than for Treatments 1,3-5.

Earthworms in general, but especially the geophages, appear to have a unique influence on the nature of K in the soil. The significantly higher values for exchangeable K in the unaltered soil for Treatment 2 likely reflects the difficulty in separation of the parts when sampling. An examination of results for the parts(Table 20) indicates that exchangeable K is significantly higher in the faecal pellets of earthworms than in the tunnel linings or unaltered soil.

The high values for exchangeable K and trends for loss of K through leaching(Appendix VIII) appear to be related to earthworms lowering the pH of the soil which possibly results in de-potassification of clay minerals. This phenomenon is most strongly expressed in soils where the geophages were present. Where exchangeable K values are the highest(faecal pellets-Table 20) pH values are also the lowest(Table 19 and 20). The pH values of the faecal pellets from the Spruce Grove soil are not significantly lower than the unaltered soil and tunnel linings in Table 20 where comparisons were made between parts. When data for the unaltered soil from all treatments for the Spruce Grove soil are examined(Table 19) it is clear that the presence of earthworms, and especially the geophages(Treatments 2 and 4), has resulted in a substantial reduction in pH. The significantly lower pH values in Treatments 2-4 in the Spruce Grove and not Cooking Lake and Ellerslie soils probably reflects the neutralizing influence of inherent concentrations of inorganic carbonates in these soils(Table 20). In the Cooking Lake and Ellerslie soils carbonates are present in high concentrations and most likely prevented the gross reductions for pH values, in the presence of earthworms, observed for the Spruce Grove soil.

Results from the leachate analysis indicate that loss of K in the presence of the geophages(Treatment 2) for all the soil types is significantly higher than for any other treatment(Appendix VIII). The high loss of K over time from Treatment 2 appears to be related to the declining pH values of the leachates.

If K was lost simply through leaching of the grass results for K concentrations in the leachates would be expected to parallel those for Na somewhat. This parallel trend did not occur. A comparison of results for K loss from the grass in Treatments 1 and 2(Table 22) indicate that a significantly higher loss of K occurred only in the Ellerslie soil where the trend for leaching loss of K is least strongly expressed.

Although inconclusive, these data suggest that the geophages may be involved in the de-potassification of clay minerals through their influence on soil reaction. Bal(1982) stated that the geophageous species he studied failed to establish successful populations in a sandy soil despite adequate moisture. He speculated they may require micaceous and other clay minerals in their diet. These clay minerals were absent in the sandy textured soil but were present in a nearby soil where the geophages successfully established themselves. To examine this question further in this study, X-ray diffraction patterns were run on clay separates from the faecal and control soil materials. No conclusive evidence for de-potassification of clay minerals could be observed in the diffraction patterns. Although it was deemed necessary to do a total dissolution analysis, in order to determine the difference(if it exists) in the amount of K present between the control soil and faecal material, the size of sample available for such an analysis was too small.

4.4.7 Summary

Although it was not a primary objective of this study to examine the role of earthworms in the cycling of Ca, Mg, Na and K, the chemical analyses of the soil, leachates and grass provides some basic information. The data, although inconclusive, provide a basis for further research.

Indications are that earthworms, in general, enhance the mobilization of these elements. Concentrations of Ca, Mg, Na and K were generally higher in the leachates from columns where earthworms were present than in the controls. Although the elements present in the leachates are considered losses in this study, they would be available for plant uptake in a natural environment where vegetation is present.

It would be inappropriate to conclude what the origin(organic vs. inorganic) is of the elements released, based on data from this study, although some inferences can be made.

Based on data for soluble inorganic carbon, carbonates, pH and extractable Ca, indications are that some Ca is released through the dissociation of carbonates where earthworms lower the soil pH. Some Ca is also released through the decomposition of grass.

In this study the concentrations of Mg in the leachates were highest where earthworms were present. Indications are this was the result of Mg released through enhanced decomposition of the grass in the presence of earthworms.

Loss of Na through leaching was also highest where earthworms were present. Exchangeable Na was lower in the faecal material from treatments where *L. terrestris* was present. This was attributed to *L. terrestris* creating an environment conducive to accelerated leaching through its tunnelling behaviour. Na, being a highly mobile ion, was preferentially leached.

Potassium data presented in this section indicates that the geophages may be involved in de-potassification of clay minerals. However, this requires further investigation.

5. SUMMARY AND CONCLUSIONS

Since detailed summaries are provided at the end of each section in the Results and Discussion this chapter will include only the major findings of the study in point form.

1. Earthworms cause alterations to soil structure but the type of changes observed are dependent on the species of earthworm and type of soil involved.
    a)*L.terrestris* played a primary role in structure development by withdrawing litter from the surface into the soil and bringing it into intimate contact with inorganic components.

    b)*O.tyrtaeum* and *A.turgida*(geophages) played a secondary role by ingesting large quantities of matrix material which was physically altered and translocated, resulting in homogenization of the soil.

    c)A synergistic effect occurred where both ecological groups co-existed. Processes initiated by *L.terrestris* were intensified by the geophages who also transported material modified by *L.terrestris* into the bulk of the soil.

    d)Significant contributions to organic plasma concentrations, which bound inorganic soil constituents together, were made by all species.

    e)Where a high proportion of clays were present earthworms increased the degree of their orientation.

f)In the silty clay loam soil granular structure developed in the presence of all species of earthworms. This was most strongly expressed where both ecological groups of earthworms co-existed.

g)Fusion of the matrix material was strongly expressed in the clay loam soil where both ecological groups of earthworms co-existed and where *L.terrestris* was active alone.

h)Weakly expressed granular structure developed where the geophages were active in the sandy loam soil. Fusion of the soil matrix occurred where *L.terrestris* was active alone in the same soil.

2. The stabilization of soil structure in the presence of earthworms is related to the concentration of clay-bound neutral sugars, but not uronic acids, in the faecal material. Where fragmoidic and granoidic fabric types developed concentrations of clay-bound neutral sugars in the faecal material were high. Where fusion of the matrix material occurred concentrations of clay-bound neutral sugars in the faecal pellets were low.
3. The influence of earthworms on decomposition was attributed to their regulation of decomposer organisms. The interaction of earthworm species with decomposer organisms and soil type were reflected in significant differences for carbon balances.

   a)All three soil types benefitted in regards to stabilized organic carbon in the presence of earthworms. In every case where earthworms were present some extractable carbon was present in the clay-bound component while in all the controls carbon was absent from the clay-bound component.

b)The sandy loam soil benefitted the most in the presence of *L.terrestris* where decomposition was retarded. In treatments where decomposition was accelerated in this soil, less carbon was stabilized and more carbon was lost to respiration.

c)All species of earthworms accelerated decomposition in the silty clay loam soil. This proved most beneficial in terms of stabilized organic carbon especially where both ecological groups of earthworms were present. Enhanced stabilization of carbon was attributed to the high percentage of smectite clay in this soil relative to the clay loam and sandy loam soils.

d)All species of earthworms accelerated decomposition in the clay loam soil which proved non-beneficial in terms of stabilized organic carbon.

4. All species of earthworms enhanced the mobilization of Ca, Mg and Na in the soil. Leaching losses of these elements were highest where *L.terrestris* was present. This was attributed to the tunnelling behavior of the earthworm which is conducive to enhanced leaching. Data for K suggest that the geophages may be involved in

de-potassification of clay minerals.

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Appendices

Appendix I

Earthworm Preservation

Earthworm Preservation(Wm. M. Fender-1982)

1. Relaxing - Place the worms in a solution containing 1 part saturated $MgSO_4$ solution(epsom salts) to 4 parts water and leave until they no longer respond to mechanical stimulus. This should take one to two hours.

2. Killing - This is best done by dipping the worms briefly(1 to 2 seconds for the smaller forms, up to 20 seconds for the larger) in Bouin's picro-formol. They should then be placed straight, but not stretched, on a flat surface for about one minute. A sheet of paper is best to absorb excess Bouin's.

3. Fixing - Place the worms in a long V-shaped container filled with Lavdowsky's Fluid(FAA), a dissecting pan elevated on one side works nicely. When the worms have stiffened, put them in a glass tube or other suitable container with fresh FAA.

4. Preservation - After several hours, overnight will do, replace the FAA with either 4% Formaldehyde or 70% Ethanol. Formaldehyde must not be allowed to touch cork or the specimens will be blackened beyond use.

BOUIN'S PICRO-FORMOL

*Picric Acid, saturated aqueous solution	75 parts
Commercial Formalin	25 parts
Acetic Acid, glacial	5 parts

*Picric acid is explosive when perfectly dry, but is safe when stored as a saturated solution. It is not necessary that all of the solid dissolve, as long as it is wet.

*LAVDOWSKY'S FLUID(FAA)

Formalin	10 parts
95% Ethanol	50 parts
Acetic Acid, glacial	1 part
Water	40 parts

*modified

Appendix II

Species Identification on Subsamples from Collection Site

Species Identification on Subsamples from Collection Site

SAMPLE NO.	SPECIES	MATURITY
1	*Lumbricus sp.(terrestris)*	*aclitellate
2	*Lumbricus terrestris*	mature
3	*Aporrectodea sp.*	immature
4	*Lumbricus terrestris*	mature
5	*Lumbricus sp.(terrestris)*	aclitellate
6	*Lumbricus terrestris*	mature
7	*Lumbricus terrestris*	young adult
8	*Octolasion tyrtaeum*	mature
9	*Octolasion tyrtaeum*	mature
10	*Octolasion tyrtaeum*	mature
11	*Aporrectodea turgida*	mature
12	*Octolasion tyrtaeum*	mature
13	*Octolasion tyrtaeum*	mature
14	*Octolasion tyrtaeum*	mature
15	*Octolasion tyrtaeum*	mature
16	*Aporrectodea turgida*	mature
17	*Octolasion tyrtaeum*	mature
18	*Octolasion tyrtaeum*	mature
19	*Octolasion tyrtaeum*	mature
20	*Octolasion tyrtaeum*	mature
21	*Aporrectodea turgida*	aclitellate
22	*Octolasion tyrtaeum*	mature
23	*Octolasion tyrtaeum*	mature
24	*Octolasion tyrtaeum*	mature
25	*Lumbricus terrestris*	aclitellate

PERCENT OF LARGE AND SMALL WORMS REPRESENTED BY EACH SPECIES

LARGE/SMALL WORMS	SPECIES	PERCENT
LARGE WORMS	*Lumbricus terrestris*	100
SMALL WORMS	*Octolasion tyrteum*	78
	Aporrectodea turgida	22

*aclitellate:no clitellum,prereproductive adult.

Appendix III

Soil Moisture and Temperature for Cooking Lake, Ellerslie and Spruce Grove Columns

Table 23:Moisture(%) and temperature(°C) of the soil in the Cooking Lake columns.

DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)	DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)
Aug.29/81	1	1	37.1	9.5	Jan.28/82	153	1	45.5	9.0
	1	2	36.4	9.0		153	2	36.4	9.0
	1	3	27.9	7.0		153	3	31.8	6.0
	1	4	29.7	7.5		153	4	33.5	7.0
Nov.28/81	1	5	37.7	-	Apr. 28/82	153	5	40.4	6.5
Sept.11/81	14	1	38.3	9.2	Feb.11/82	167	1	45.1	7.5
	14	2	39.0	9.2		167	2	37.4	8.0
	14	3	28.7	6.5		167	3	32.3	6.0
	14	4	30.8	7.0		167	4	31.9	6.0
Dec.11/81	14	5	-	-	May 11/82	165	5	40.4	6.2
Sept.28/81	31	1	39.6	9.0	Mar. 1/82	185	1	44.0	7.0
	31	2	39.6	9.0		185	2	35.7	8.0
	31	3	29.5	6.0		185	3	32.1	7.0
	31	4	31.3	7.0		185	4	33.1	7.0
Dec.29/81	32	5	39.0	7.5	May 28/82	182	5	40.4	6.5
Oct.13/81	46	1	40.4	9.0	Mar.11/82	195	1	46.6	7.0
	46	2	40.4	8.5		195	2	38.9	8.0
	46	3	30.1	6.0		195	3	32.6	6.0
	46	4	31.9	6.8		195	4	33.4	6.0
Jan.11/82	45	5	40.4	7.2	June 11/82	196	5	-	-
Oct.28/81	61	1	41.6	7.5	Mar.28/82	212	1	43.8	7.0
	61	2	41.2	7.0		212	2	36.8	8.0
	61	3	30.3	6.0		212	3	32.6	6.0
	61	4	32.1	6.5		212	4	33.4	6.0
Jan.28/82	62	5	40.8	7.5	June 28/82	213	5	40.4	6.5

DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)	DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)
Nov.11/81	75	1	41.8	8.5	Apr. 12/82	227	1	46.6	7.0
	75	2	41.2	8.0		227	2	41.5	8.0
	75	3	30.3	6.0		227	3	32.8	6.0
	75	4	32.1	6.2		227	4	33.7	6.0
Feb.11/82	76	5	40.0	8.0	July 11/82	226	5	40.4	6.0
Nov.28/81	92	1	42.3	8.5	Apr. 28/82	243	1	44.0	6.5
	92	2	42.8	8.0		243	2	44.6	7.0
	92	3	31.0	6.0		243	3	32.6	6.0
	92	4	32.5	6.2		243	4	33.7	6.0
Feb.28/82	93	5	40.4	7.5	July 28/82	244	5	40.0	6.5
Dec.11/81	105	1	-	-	May 11/82	257	1	44.8	6.8
	105	2	-	-		257	2	47.8	7.0
	105	3	-	-		257	3	32.8	6.0
	105	4	-	-		257	4	33.7	6.0
Mar.11/82	104	5	39.4	7.0	Aug. 11/82	258	5	39.5	6.0
Dec.29/81	123	1	44.0	10.0	May 28/82	274	1	44.8	7.0
	123	2	45.4	10.0		274	2	47.8	7.0
	123	3	31.5	6.5		274	3	32.6	6.0
	123	4	33.2	7.0		274	4	33.4	6.0
Mar.28/82	121	5	40.0	7.0	Aug.28/82	275	5	40.2	6.0
Jan.11/82	136	1	45.8	10.0					
	136	2	47.0	9.5					
	136	3	31.9	6.0					
	136	4	33.4	6.8					
Apr. 12/82	136	5	39.4	7.0					

Table 24:Moisture(%) and temperature(°C) of the soil in the Ellerslie columns.

DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)	DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)
Sept.1/81	1	1	42.2	10.0	Feb.8/82	160	1	34.5	7.0
	1	2	42.8	10.5		160	2	55.7	8.0
	1	3	39.0	7.2		160	3	39.8	6.2
	1	4	31.0	7.2		160	4	37.7	6.5
Nov.30/81	1	5	-	-	May 1/82	150	5	-	-
Sept.16/81	16	1	48.6	9.5	Feb.14/82	166	1	34.1	7.0
	16	2	48.6	10.0		166	2	55.7	7.5
	16	3	39.9	6.5		166	3	39.6	6.0
	16	4	36.4	7.0		166	4	37.4	6.0
Dec.14/81	14	5	35.8	8.0	May 14/82	163	5	44.5	7.2
Oct.5/81	35	1	41.2	10.0	Mar.1/82	181	1	32.8	7.0
	35	2	41.9	10.0		181	2	55.7	8.0
	35	3	34.4	7.0		181	3	39.4	6.0
	35	4	31.6	7.5		181	4	37.1	7.0
Jan.2/82	32	5	35.7	7.5	June 2/82	182	5	42.5	6.5
Oct.14/81	44	1	41.2	10.5	Mar.14/82	194	1	26.8	7.0
	44	2	39.5	10.5		194	2	55.7	8.0
	44	3	33.4	6.0		194	3	38.7	6.0
	44	4	32.8	6.5		194	4	38.8	6.0
Jan.14/82	44	5	47.7	8.0	June 16/82	196	5	42.3	7.0
Nov.2/81	62	1	41.2	8.5	Apr. 1/82	212	1	39.1	6.5
	62	2	37.9	9.0		212	2	59.0	8.0
	62	3	34.9	6.0		212	3	38.7	6.0
	62	4	33.5	7.0		212	4	38.2	6.0
Feb.8/82	68	5	44.4	7.5	July 1/82	211	5	42.0	6.2

DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)	DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)
Nov. 15/81	75	1	42.7	9.0	Apr. 13/82	224	1	40.8	7.0
	75	2	52.0	9.5		224	2	55.7	7.5
	75	3	39.0	6.0		224	3	39.0	6.0
	75	4	34.5	7.0		224	4	38.4	6.0
Feb. 14/82	74	5	43.7	7.8	July 14/82	224	5	44.2	6.5
Dec. 1/81	91	1	43.2	9.0	May 1/82	242	1	-	-
	91	2	52.4	9.5		242	2	-	-
	91	3	38.8	6.0		242	3	-	-
	91	4	35.4	7.0		242	4	-	-
Mar. 1/82	89	5	41.8	7.5	Aug. 1/82	242	5	42.5	7.5
Dec. 14/81	104	1	38.0	8.5	May 14/82	255	1	42.5	7.1
	104	2	54.8	9.0		255	2	52.4	8.0
	104	3	37.8	6.5		255	3	39.7	6.0
	104	4	37.6	7.0		255	4	39.2	6.1
Mar. 14/82	102	5	40.2	8.0	Aug. 14/82	255	5	46.3	7.0
Jan. 2/82	123	1	36.7	10.0	June 2/82	274	1	43.9	6.0
	123	2	55.7	10.0		274	2	59.0	6.5
	123	3	38.4	6.0		274	3	39.6	6.0
	123	4	37.6	7.0		274	4	38.4	6.0
Apr. 1/82	120	5	40.2	7.0	Sept. 1/82	273	5	47.1	7.0
Jan. 14/82	135	1	37.2	8.8					
	135	2	55.7	9.0					
	135	3	40.7	6.0					
	135	4	40.2	6.6					
Apr. 13/82	132	5	39.6	7.0					

Table 25:%Moisture(%) and temperature(°C) of the soil in the Spruce Grove columns.

DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)	DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)
July 17/81	1	1	21.1	10.0	Jan.9/82	187	1	25.1	8.5
	1	2	25.0	10.0		187	2	35.1	8.0
	1	3	17.5	6.0		187	3	21.9	6.5
	1	4	16.7	7.0		187	4	21.0	7.0
Oct.8/81	1	5	20.7	-	Apr. 10/82	185	5	20.3	-
July 21/81	15	1	23.0	9.5	Jan.23/82	201	1	24.7	8.0
	15	2	25.0	9.5		201	2	35.1	7.0
	15	3	17.4	6.0		201	3	22.0	6.0
	15	4	16.6	6.8		201	4	23.7	6.2
Oct.23/81	16	5	21.0	-	Apr. 24/82	199	5	20.0	-
Aug.6/81	31	1	26.8	10.0	Feb.8/82	217	1	22.7	8.0
	31	2	24.1	10.0		217	2	33.4	6.0
	31	3	17.1	7.0		217	3	21.9	6.0
	31	4	17.4	8.0		217	4	23.6	7.0
Nov.8/81	32	5	21.1	-	May 6/82	212	5	20.2	-
Aug.24/81	49	1	22.9	7.6	Feb.22/82	231	1	24.0	7.0
	49	2	27.6	7.0		231	2	33.4	6.0
	49	3	17.2	6.0		231	3	22.0	6.0
	49	4	17.9	6.8		231	4	25.3	7.0
Nov.22/81	46	5	20.5	-	May 22/82	228	5	20.2	-
Sept.8/81	64	1	22.3	9.5	Mar.8/82	245	1	22.7	8.0
	64	2	28.6	9.5		245	2	33.4	7.0
	64	3	17.3	6.0		245	3	22.3	7.0
	64	4	18.2	6.5		245	4	26.0	7.0
Dec.9/81	63	5	20.6	-	June 6/82	243	5	20.2	-
Sept.22/81	78	1	23.6	9.5	Mar.22/82	259	1	22.6	7.5
	78	2	29.1	9.0		259	2	33.4	6.0
	78	3	18.6	6.0		259	3	22.2	6.0
	78	4	18.8	7.0		259	4	24.2	7.0
Dec.22/81	76	5	20.2	-	June 22/82	259	5	20.2	-

DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)	DATE	CUMULATIVE TIME(DAYS)	COLUMN NUMBER	PERCENT MOISTURE	TEMP. (°C)
Oct.8/81	94	1	23.7	9.0	Apr. 10/82	278	1	21.8	7.0
	94	2	29.7	8.5		278	2	33.4	6.0
	94	3	19.5	5.8		278	3	22.2	6.0
	94	4	19.7	6.0		278	4	24.2	6.5
Jan.9/82	94	5	20.8	-	July 8/82	275	5	19.4	-
Oct.23/81	109	1	23.6	7.0	Apr. 24/82	292	1	23.2	7.0
	109	2	30.4	6.0		292	2	33.4	6.0
	109	3	20.2	6.2		292	3	22.2	6.0
	109	4	20.8	7.2		292	4	24.2	7.0
Jan.23/82	108	5	20.7	-	July 22/82	289	5	19.8	-
Nov.8/81	125	1	23.5	7.2	May 6/82	304	1	23.2	7.0
	125	2	31.0	6.8		304	2	33.4	6.0
	125	3	20.5	6.5		304	3	22.3	6.0
	125	4	21.2	7.0		304	4	24.1	7.0
Feb.8/82	124	5	20.8	-	Aug.8/82	306	5	19.8	-
Nov.22/81	139	1	23.9	8.8	May 22/82	320	1	24.5	7.5
	139	2	31.8	7.8		320	2	34.1	6.0
	139	3	20.8	5.9		320	3	22.2	6.5
	139	4	22.0	6.2		320	4	24.2	7.0
Feb.22/82	138	5	20.2	-	Aug.22/82	320	5	19.4	-
Dec.9/81	156	1	24.1	8.8	June 6/82	335	1	24.5	7.5
	156	2	33.4	7.8		335	2	33.4	6.0
	156	3	24.0	6.0		335	3	22.3	6.5
	156	4	22.3	6.2		335	4	23.8	7.5
Mar.8/82	152	5	20.4	-	Sept.8/82	337	5	19.6	-
Dec.22/81	169	1	25.0	9.0					
	169	2	32.0	8.0					
	169	3	21.6	6.0					
	169	4	23.4	6.2					
Mar.22/82	166	5	20.2	-					

Appendix IV

Weight of Soil and Earthworms added to Spruce Grove, Ellerslie and Cooking Lake Columns

Table 26: Weight of soil and earthworms added to Cooking Lake columns.

COLUMN NO.	SOIL ADDED (g. o.d.)	SOIL COLUMN HEIGHT(cm.)	SOIL Db (g/cm^3)	*L.terrestris* WEIGHT(gm.)	*O. tyrtaeum* *A. turgida* WEIGHT(gm.)
C.L.1A	210.0	4.1	1.12		
C.L.1B	164.0	3.7	0.97		
C.L.1C	163.0	3.3	1.08		
C.L.2A	211.0	4.4	1.05		1.23 0.53 0.45 1.29 0.97
C.L.2B	124.0	3.2	0.85		1.59 0.93 0.78 1.10 1.01
C.L.2C	141.0	3.5	0.88		1.45 0.68 0.78 1.01 0.72

COLUMN NO.	SOIL ADDED (g. o.d.)	SOIL COLUMN HEIGHT(cm.)	SOIL Db (g/cm^3)	*L. terrestris* WEIGHT(gm.)	*O. tyrtaeum* *A. turgida* WEIGHT(gm.)
C.L.3A	2897.0	49.3	1.29	4.52 5.21	
C.L.3B	2867.0	49.3	1.28	4.89 4.48	
C.L.3C	2917.0	49.9	1.28	4.56 5.37	
C.L.4A	2860.0	48.8	1.28	4.43 4.26	0.46 0.94 0.71 0.74 0.72
C.L.4B	2754.0	48.4	1.25	5.14 4.23	1.56 0.97 0.87 0.55 1.16
C.L.4C	2826.0	48.5	1.28	4.57 5.25	0.93 1.02 1.33 0.56 0.92
C.L.5A	244.0	4.2	1.51		
C.L.5B	245.0	4.2	1.52		
C.L.5C	245.0	4.1	1.55		

Table 27: Weight of soil and earthworms added to the Ellerslie columns.

COLUMN NO.	SOIL ADDED (g. o.d.)	SOIL COLUMN HEIGHT(cm.)	SOIL Db (g/cm^3)	*L. terrestris* WEIGHT(gm.)	*O. tytaeum* *A. turgida* WEIGHT(gm.)
E.1A	201.0	4.3	1.02		
E.1B	140.0	3.5	0.88		
E.1C	138.0	3.4	0.89		
E.2A	200.0	4.5	0.98		0.45 0.77 0.82 1.07 0.99
E.2B	139.0	3.2	0.95		0.68 0.79 1.28 1.42 0.94
E.2C	138.0	3.4	0.89		0.64 1.00 0.69 1.17 0.88

COLUMN NO.	SOIL ADDED (g. o.d.)	SOIL COLUMN HEIGHT(cm.)	SOIL Db (g/cm^3)	*L.terrestris* WEIGHT(gm.)	*O. tyrtaeum* *A. turgida* WEIGHT(gm.)
E.3A	2982.0	49.5	1.32	4.12 4.55	
E.3B	2932.0	49.5	1.30	5.87 4.45	
E.3C	2941.0	47.7	1.35	5.21 5.30	
E.4A	2907.0	48.9	1.30	4.98 4.02	0.94 1.06 1.14 0.88 1.12
E.4B	2903.0	48.0	1.33	4.09 5.58	0.43 1.05 1.20 0.96 1.13
E.4C	2922.0	49.4	1.30	4.82 4.79	1.13 0.62 1.21 0.87 0.96
E.5A	222.7	4.5	1.29		
E.5B	208.3	4.3	1.26		
E.5C	223.3	4.5	1.29		

Table 28: Weight of soil and earthworms added to the Spruce Grove columns.

COLUMN NO.	SOIL ADDED (g. o.d.)	SOIL COLUMN HEIGHT(cm.)	SOIL Db (g/cm^3)	*L.terrestris* WEIGHT(gm.)	*O. tyrtaeum* *A. turgida* WEIGHT(gm.)
S.G.1A	229.0	4.7	1.27		
S.G.1B	248.0	5.2	1.24		
S.G.1C	242.0	4.7	1.34		
S.G.2A	179.0	4.1	1.13		0.99
					1.29
					1.32
					1.33
					0.96
S.G.2B	238.0	4.5	1.38		1.38
					1.35
					1.05
					1.17
					0.63
S.G.2C	241.0	4.7	1.33		0.96
					0.83
					1.95
					1.24
					1.31

COLUMN NO.	SOIL ADDED (g. o.d.)	SOIL COLUMN HEIGHT(cm.)	SOIL Db (g/cm^3)	*L.terrestris* WEIGHT(gm.)	*O. tyrtaeum* *A. turgida* WEIGHT(gm.)
S.G.3A	2408.0	47.2	1.33	4.18 2.18	
S.G.3B	2299.0	46.5	1.28	3.41 2.28	
S.G.3C	2384.0	46.0	1.35	3.20 3.12	
S.G.4A	2366.0	46.2	1.33	4.07 2.27	1.19 0.74 1.18 1.01 1.02
S.G.4B	2362.0	46.2	1.33	3.21 2.53	1.30 0.94 0.74 1.33 1.15
S.G.4C	2289.0	45.5	1.31	4.52 2.11	0.50 0.65 0.93 1.08 0.72
S.G.5A	278.0	5.4	1.34		
S.G.5B	279.0	4.9	1.48		
S.G.5C	278.0	4.9	1.48		

Appendix V

Replacement Earthworms Added to Soil Columns

Table 29: Replacement earthworms added to soil columns subsequent to the initiation of the experiment.

Date	Column Number	Type of Addition	Weight of Addition (gms.)
Dec. 1/81	E 3A	*L. terrestris*	2.00 2.20
	E 4B	*L. terrestris*	2.05 1.99
		O. tyrtaeum/ A. turgida	0.52 0.55 0.13 0.30
	E 4C	*L. terrestris*	2.05 3.67
		O. tyrtaeum/ A. turgida	0.35 0.38 0.88 0.63
Jan.25/82	E 4B	*L.terrestris*	2.80
	E 4C	*L. terrestris*	2.58
Jan. 6/82	E 2A	*O. tyrtaeum/ A. turgida*	0.59 0.29 0.43 0.65
	E 2B	*O. tyrtaeum/ A. turgida*	0.43 0.40 0.10 0.10
	E 2C	*O. tyrtaeum/*	0.79 0.80 0.39 0.25
	E 4A	*O. tyrtaeum/ A. turgida*	0.19 0.28 0.59
	E 4B	*O. tyrtaeum/ A. turgida*	0.60 0.48 0.40
	E 4C	*O. tyrtaeum/ A. turgida*	0.54 0.50 0.20
	C.L.4A	*O. tyrtaeum/ A. turgida*	0.19 0.48
	C.L.4B	*O. tyrtaeum/ A. turgida*	0.52 0.55 0.13
	C.L.4C	*O. tyrtaeum/ A. turgida*	0.43 0.47

Appendix VI

Recipes for Media used in Microbiological Assays

Recipes for Media used in Microbiological Assays

1. M77(Base Medium 77 for Azotobacter-nitrogen free)

K_2HPO_4	0.5 gm.	$FeCl_3$	trace
$MgSO_4$	0.2 gm.	Mannitol	5.0 gm.
NaCl	0.2 gm.	Sucrose	5.0 gm.
$MnSO_4$	trace	$CaCO_3$	3.0 gm.
Distilled water	1000 mls.		

2. Butlins Medium

K_2HPO_4	0.5 gm.	$CaCl_2 \cdot 6H_2O$	0.1 gm.
NH_4Cl	1.0 gm.	$MgSO_4 \cdot 7H_2O$	1.0 gm.
Yeast extract	1.0 gm.	$FeSO_4$	0.002 gm.
Na_2SO_4	2.0 gm.		
Na lactate	3.5 gm. (60% solution)=2.5 ml.		
Distilled water	1000 mls.		
final pH	7.5		

3. Lactose Broth

Nutrient broth	8.0 gm.
Lactose	5.0 gm.
Phenol red	0.018 gm.
Distilled water	1000 ml.
final pH	7.5

4. Rose Bengal-Streptomycin Agar

Glucose(Dextrose)	10.0 gm.	KH_2PO_4	1.0 gm.
Peptone	5.0 gm.	$MgSO_4 \cdot 7H_2O$	0.5 gm.
Agar	15.0 gm.		
Rose bengal	0.033 gm.(1 ml. of standard solution)		
Distilled water	1000 mls.		

Sterilize by autoclaving. When ready to pour add streptomycin to give final concentration of 30 ug/ml. (6 ml. of standard solution/1000 ml.).

5. #1 Medium

Tryptone	2.0 gm.
Agar	10.0 gm.
Distilled water	1000 ml.

6. Skimmed Milk Medium

Skimmed milk	1.0 gm.
Yeast extract	0.1 gm.
Agar	3.0 gm.
Distilled water	1000 ml.

7. Yeast Agar

Granular yeast	2.5 gm.
Agar	7.5 gm.
Distilled water	1000 mls.

8. PCA

Tryptone	5.0 gm.
Yeast extract	2.5 gm.
Glucose	1.0 gm.
Agar	15.0 gm.
Distilled water	1000 ml.

9. FVM

Malic acid	5.0 gm.	NaCl	0.1 gm.
KOH	4.0 gm.	$CaCl_2$	0.02 gm.
K_2HPO_4	0.5 gm.	$Fe_2SO_4 \cdot 7H_2O$	0.5 gm.
$MgSO_4 \cdot 7H_2O$	0.2 gm.	$NaMoO_4 \cdot 2H_2O$	0.002 gm.
$MnSO_4 \cdot H_2O$	0.01 gm.		
Distilled water	1000 ml.		
.5% alcoholic solution of bromothymol blue			2.0 ml.
final pH	6.8		

Appendix VII

Calculations for Carbon Balances

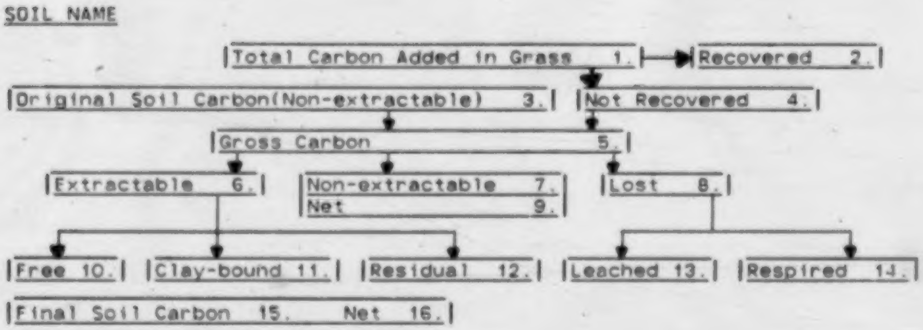
SOIL NAME
Total Carbon Added in Grass 1.
Recovered 2.
Original Soil Carbon(Non-extractable) 3.
Not Recovered 4.
Gross Carbon 5.
Extractable 6.
Non-extractable 7.
Net 9.
Lost 8.
Free 10.
Clay-bound 11.
Residual 12.
Leached 13.
Respired 14.
Final Soil Carbon 15. Net 16.

Figure 16:Guide to box numbers in models.
(see following pages)

Guide to the Origin of Numerical Values in Carbon Balances

Column Number	Origin of Value	Box Number in Model
1	Determined	
2	Determined	
3	Calculated Col.1-Col.2	
4	Calculated Col.1x(47/100) (%C in grass)	1
5	Calculated Col.2x(47/100)	2
6	Calculated Col.3x(47/100)	4
7	Determined	
8	Determined	
9	Determined	
10	Calculated (Col.7x1000xCol.8)/100	3
11	Calculated Col.6+Col.10(total)	5
12	Calculated (Col.7x1000xCol.9)/100	15
13	Calculated Col.11-Col.12(total)	8
14	Calculated Col.12-Col.10	16

Column Number	Origin of Value	Box Number in Model
15	Determined	
16	Determined	
17	Determined	
18	Calculated ((Col.15xCol.7)/1000) x(40/100)(%C in glucose)	10(total)
19	Calculated ((Col.16xCol.7)/1000) x(40/100)(%C in glucose)	11(total)
20	Calculated ((Col.17xCol.7)/1000) x(40/100)(%C in glucose)	12(total)
21	Calculated Sum of totals across Col.18-Col.20	6
22	Determined	13
23	Calculated Col.12-Col.21	7
24	Calculated Col.23-Col.10(total)	9
25	Calculated Col.13-Col.22	14

Table 30:Calculations for the carbon balance for the Spruce Grove soil.

Treatment Number	Col.1 Grass Added to columns(mg)	Col.2 Grass recovered(mg)	Col.3 Grass not recovered(mg)	Col.4 Carbon in grass added(mg)	Col.5 Carbon in grass recovered(mg)	Col.6 Carbon in grass not recovered(mg)
1	6000	2591	3409	2820	1218	1602
2	6000	1808	4192	2820	850	1970
3	6000	342	5658	2820	161	2659
4	6000	368	5632	2820	173	2647

Treatment Number	Part	Col.7 Soil weight gr.(O.D.)	Col.8 Original % C	Col.9 Final % C	Col.10 Original Total C(mg)	Col.11 Gross Total C(mg)
1	Unaltered Soil	816	.125	.195	1020	2622
2	Unaltered Soil	694	.125	.220	868	
	Tunnel Linings	80	.125	.350	100	
	Faecal Pellets	12	.125	.835	15	
	Total	786			983	2953
3	Unaltered Soil	2699	.125	.185	3374	
	Tunnel Linings	266	.125	.390	332	
	Faecal Pellets	9	.125	1.280	11	
	Total	2974			3717	6376
4	Unaltered Soil	2554	.125	.165	3192	
	Tunnel Linings	374	.125	.340	468	
	Faecal Pellets	14	.125	.900	18	
	Total	2942			3678	6325

Treatment Number	Part	Col. 12 Final Total C(mg)	Col. 13 Carbon lost(mg)	Col. 14 Net loss(-) or gain(+) in C(mg)	Col. 15 Free glucose eq. (ug g^{-1})	Col. 16 Clay-bound glucose eq. (ug g^{-1})
1	Unaltered Soil	1591	1040	+ 571	0	0
2	Unaltered Soil	1527		+ 659	0	95
	Tunnel Linings	280		+ 180	106	0
	Faecal Pellets	100		+ 85	750	492
	Total	1907	1960	+ 925		
3	Unaltered Soil	4993		+1619	0	390
	Tunnel Linings	1037		+ 705	318	318
	Faecal Pellets	115		+ 104	1650	308
	Total	6145	240	+2428		
4	Unaltered Soil	4214		+1022	0	0
	Tunnel Linings	1272		+ 805	0	0
	Faecal Pellets	126		+ 108	1650	664
	Total	5612	721	+1934		

Treatment Number	Part	Col.17 Residual glucose eq. (ug g^{-1})	Col.18 Free C in glucose eq. (ug g^{-1})	Col.19 Clay-bound C in glucose eq.(mg)	Col.20 Residual C in glucose eq.(mg)
1	Unaltered Soil	382	0	0	125
2	Unaltered Soil	0	0	26	0
	Tunnel Linings	861	3	0	28
	Faecal Pellets	1640	4	2	8
	Total		7	28	36
3	Unaltered Soil	0	0	421	0
	Tunnel Linings	114	34	34	12
	Faecal Pellets	2490	6	1	9
	Total		40	456	21
4	Unaltered Soil	0	0	0	0
	Tunnel Linings	0	0	0	0
	Faecal Pellets	1700	9	4	10
	Total		9	4	10

Treatment Number	Col.21 Total Extractable C (mg)	Col.22 Total Soluble C in leachates(mg)	Col.23 Total Non-extractable C (mg)	Col.24 Net loss(-) or gain(+) in Non-extractable C (mg)	Col.25 C lost to respiration(mg)
1	125	9	1457	+ 437	1031
2	71	14	1822	+ 839	1046
3	517	9	5619	+1902	231
4	23	8	5581	+1903	713

Table 31:Calculations for the carbon balance for the Cooking Lake soil.

Treatment Number	Col.1 Grass Added to columns(mg)	Col.2 Grass recovered(mg)	Col.3 Grass not recovered(mg)	Col.4 Carbon in grass added(mg)	Col.5 Carbon in grass recovered(mg)	Col.6 Carbon in grass not recovered(mg)
1	5000	1919	3081	2350	902	1448
2	5000	996	4004	2350	468	1882
3	5000	357	4643	2350	168	2182
4	5000	183	4817	2350	86	2264

Treatment Number	Part	Col.7 Soil weight gr.(O.D.)	Col.8 Original % C	Col.9 Final % C	Col.10 Original Total C(mg)	Col.11 Gross Total C(mg)
1	Unaltered Soil	690	1.245	1.224	8590	10038
2	Unaltered Soil	560	1.245	1.167	6972	
	Tunnel Linings	94	1.245	1.220	1170	
	Faecal Pellets	18	1.245	1.755	224	
	Total	672			8366	10248
3	Unaltered Soil	3147	1.245	1.132	39180	
	Tunnel Linings	196	1.245	1.407	2440	
	Faecal Pellets	44	1.245	2.145	548	
	Total	3387			43168	44350
4	Unaltered Soil	2802	1.245	1.208	34884	
	Tunnel Linings	500	1.245	1.384	6225	
	Faecal Pellets	9	1.245	1.675	112	
	Total	3311			41221	43485

Treatment Number	Part	Col.12 Final Total C(mg)	Col.13 Carbon lost(mg)	Col.14 Net loss(-) or gain(+) in C (mg)	Col.15 Free glucose eq. (ug g^{-1})	Col.16 Clay-bound glucose eq. (ug g^{-1})
1	Unaltered Soil	8446	1592	- 144	0	0
2	Unaltered Soil	6535		- 435	0	244
	Tunnel Linings	1147		- 23	533	212
	Faecal Pellets	316		+ 92	1620	605
	Total	7998	2250	- 368		
3	Unaltered Soil	35624		-3556	314	0
	Tunnel Linings	2758		+ 318	0	410
	Faecal Pellets	944		+ 396	2205	387
	Total	39326	5021	-2842		
4	Unaltered Soil	33848		-1036	284	0
	Tunnel Linings	6920		+ 695	349	574
	Faecal Pellets	151		+ 39	1584	188
	Total	40919	2566	- 302		

Treatment Number	Part	Col.17 Residual glucose eq. (ug g^{-1})	Col.18 Free C in glucose eq. (ug g^{-1})	Col.19 Clay-bound C in glucose eq.(mg)	Col.20 Residual C in glucose eq.(mg)
1	Unaltered Soil	1104	0	0	305
2	Unaltered Soil	1126	0	55	252
	Tunnel Linings	1012	20	8	38
	Faecal Pellets	3225	12	4	7
	Total		32	67	297
3	Unaltered Soil	656	395	0	1218
	Tunnel Linings	295	0	32	23
	Faecal Pellets	4080	38	7	71
	Total		433	39	1312
4	Unaltered Soil	215	318	0	241
	Tunnel Linings	1068	70	115	214
	Faecal Pellets	2835	6	1	10
	Total		395	116	465

Treatment Number	Col.21 Total Extractable C (mg)	Col.22 Total Soluble C in leachates(mg)	Col.23 Total Non-extractable C (mg)	Col.24 Net loss(-) or gain(+) in Non-extractable C (mg)	Col.25 C lost to respiration(mg)
1	305	8	8148	- 442	1584
2	396	7	7602	- 764	2243
3	1784	16	37542	-4626	5005
4	975	15	39944	-1277	2551

Table 32:Calculations for the carbon balance for the Ellerslie soil.

Treatment Number	Col.1 Grass Added to columns(mg)	Col.2 Grass recovered(mg)	Col.3 Grass not recovered(mg)	Col.4 Carbon in grass added(mg)	Col.5 Carbon in grass recovered(mg)	Col.6 Carbon in grass not recovered(mg)
1	5000	2417	2583	2350	1136	1214
2	5000	1328	3672	2350	624	1726
3	5000	326	4674	2350	153	2197
4	5000	451	4549	2350	212	2138

Treatment Number	Part	Col.7 Soil weight gr.(O.D.)	Col.8 Original % C	Col.9 Final % C	Col.10 Original Total C(mg)	Col.11 Gross Total C(mg)
1	Unaltered Soil	656	.545	.595	3575	4789
2	Unaltered Soil	578	.545	.610	3150	
	Tunnel Linings	70	.545	.825	382	
	Faecal Pellets	9	.545	1.510	49	
	Total	657			3581	5307
3	Unaltered Soil	3371	.545	.500	18327	
	Tunnel Linings	57	.545	1.035	311	
	Faecal Pellets	16	.545	1.795	87	
	Total	3444			18770	20967
4	Unaltered Soil	3226	.545	.520	17582	
	Tunnel Linings	144	.545	.750	785	
	Faecal Pellets	22	.545	1.975	120	
	Total	3392			18487	20625

Treatment Number	Part	Col.12 Final Total C(mg)	Col.13 Carbon lost(mg)	Col.14 Net loss(-) or gain(+) in C (mg)	Col.15 Free glucose eq. (ug g^{-1})	Col.16 Clay-bound glucose eq. (ug g^{-1})
1	Unaltered Soil	3903	886	+ 328	0	0
2	Unaltered Soil	3526		+ 376	93	0
	Tunnel Linings	578		+ 196	92	170
	Faecal Pellets	136		+ 87	984	748
	Total	4240	1067	+ 659		
3	Unaltered Soil	16855		-1517	179	92
	Tunnel Linings	590		+ 279	0	179
	Faecal Pellets	287		+ 200	2085	1000
	Total	17732	3235	-1038		
4	Unaltered Soil	16775		- 807	0	275
	Tunnel Linings	1080		+ 295	0	95
	Faecal Pellets	434		+ 315	3030	625
	Total	18289	2336	- 198		

Treatment Number	Part	Col.17 Residual glucose eq. (ug g^{-1})	Col.18 Free C in glucose eq. (ug g^{-1})	Col.19 Clay-bound C in glucose eq.(mg)	Col.20 Residual C in glucose eq.(mg)
1	Unaltered Soil	306	0	0	80
2	Unaltered Soil	116	22	0	27
	Tunnel Linings	598	2	4	16
	Faecal Pellets	1860	4	3	7
	Total		28	7	50
3	Unaltered Soil	0	241	124	0
	Tunnel Linings	1160	0	4	27
	Faecal Pellets	2540	13	6	16
	Total		254	134	43
4	Unaltered Soil	0	0	355	0
	Tunnel Linings	360	0	6	21
	Faecal Pellets	3230	27	6	28
	Total		9	4	10

Treatment Number	Col.21 Total Extractable C (mg)	Col.22 Total Soluble C in leachates(mg)	Col.23 Total Non-extractable C (mg)	Col.24 Net loss(-) or gain(+) in Non-extractable C (mg)	Col.25 C lost to respiration(mg)
1	80	4	3823	+ 328	882
2	85	10	4155	+ 659	1057
3	431	9	17301	-1038	3226
4	443	7	17846	- 198	2329

Appendix VIII

Chemical Analysis of Leachates

Table 33:Mean values for Ca(ug/ml) in the leachates from the Spruce Grove, Cooking Lake and Ellerslie soil columns.

(values within soil types not underlain by similar letters are significantly different, P=.05)

		TREATMENT NUMBER				
SOIL TYPE	TIME (Months)	1	2	3	4	5
SPRUCE GROVE	2	21.6 ef	29.4 ef	25.9 ef	28.5 ef	17.7 ef
	8	73.1 cde	106.9 abc	48.7 def	89.8 bcd	11.3 f
	11	109.0 abc	141.7 a	109.7 abc	133.0 ab	10.5 f
COOKING LAKE	2	46.8 bc	38.5 c	77.0 abc	83.6 abc	38.5 c
	8	100.9 ab	123.7 a	82.0 abc	81.8 abc	57.1 abc
	10	122.3 a	121.7 a	123.3 a	91.7 abc	50.4 bc
ELLERSLIE	2	83.9 cd	71.6 cd	348.0 a	341.8 a	23.9 d
	8	38.7 d	77.5 cd	80.1 cd	83.4 cd	33.0 d

Table 34: Mean values for soluble inorganic carbon(ug/ml) in the leachates from the Spruce Grove, Cooking Lake and Ellerslie soil columns.

(values within soil types not underlain by similar letters are significantly different, P=.05)

		TREATMENT NUMBER				
SOIL TYPE	TIME (Months)	1	2	3	4	5
SPRUCE GROVE	2	9 b	16 b	11 b	14 b	2 a
	8	8 ab	2 a	9 b	7 b	6 ab
	11	10 b	0 a	7 b	7 b	5 a
COOKING LAKE	2	23 a	20 a	22 a	26 a	18 a
	8	26 ab	14 a	52 c	34 bc	33 bc
	10	27 b	16 a	46 d	40 cd	33 bc
ELLERSLIE	2	13 a	22 b	19 b	22 b	11 a
	8	7 a	7 a	16 a	17 a	18 a

Table 35: Mean pH values of the leachates from the Spruce Grove, Cooking Lake and Ellerslie soil columns.

(values within soil types not underlain by similar letters are significantly different, P=.05)

		TREATMENT NUMBER				
SOIL TYPE	TIME (Months)	1	2	3	4	5
SPRUCE GROVE	2	7.3 abc	7.6 ab	7.6 ab	7.6 ab	7.0 abc
	8	7.5 abc	6.8 bc	7.6 ab	7.5 abc	7.2 abc
	11	7.6 ab	6.0 d	7.4 abc	7.6 ab	6.9 bc
COOKING LAKE	2	8.2 a	8.1 a	8.4 a	8.3 a	8.4 a
	8	8.1 a	8.0 a	8.2 a	8.5 a	8.4 a
	10	8.0 a	7.6 a	8.6 a	8.4 a	7.9 a
ELLERSLIE	2	8.2 abc	8.4 ab	8.1 abc	8.2 abc	8.0 bcd
	8	7.7 cd	7.6 d	8.6 a	8.4 ab	8.3 ab

Table 36:Mean values for Mg(ug/ml) in the leachates
the Spruce Grove, Cooking Lake and
Ellerslie soil columns.

(values within soil types not underlain by similiar
letter are significantly different, P=.05)

SOIL TYPE	TIME (Months)	TREATMENT NUMBER 1	2	3	4	5
SPRUCE GROVE	2	4.9 ab	6.7 c	5.9 bc	6.6 c	4.1 a
	8	16.8 bc	27.3 c	11.3 ab	20.4 bc	2.7 a
	11	24.4 b	21.8 b	24.8 b	30.0 b	1.9 a
COOKING LAKE	2	10.0 a	8.4 a	18.0 ab	23.7 b	8.6 a
	8	24.3 b	25.1 b	30.8 b	26.8 b	12.6 a
	10	27.0 b	24.3 b	34.9 c	24.9 b	11.5 a
ELLERSLIE	2	19.4 a	20.0 a	76.6 b	78.5 b	5.0 a
	8	8.7 a	16.5 ab	22.1 b	22.8 b	7.2 a

Table 37:Mean values for Na(ug/ml) in the leachates from the Spruce Grove, Cooking Lake and Ellerslie soil columns.

(values within soil types not underlain by similar letters are significantly different, P=.05)

		TREATMENT NUMBER				
SOIL TYPE	TIME (Months)	1	2	3	4	5
SPRUCE GROVE	2	8.3 a	10.3 a	8.5 a	8.3 a	7.3 a
	8	9.0 ab	10.5 bc	8.6 b	12.0 c	5.6 a
	11	8.4 b	11.3 b	11.8 b	13.9 b	3.8 a
COOKING LAKE	2	6.2 a	4.5 a	9.2 b	9.1 b	4.8 a
	8	6.2 a	4.9 a	10.9 c	8.8 b	4.7 a
	10	6.2 b	4.7 ab	11.1 c	9.4 c	1.1 a
ELLERSLIE	2	25.7 b	29.4 b	59.0 c	57.5 c	8.7 a
	8	12.3 a	13.2 a	37.6 b	34.7 b	12.1 a

Table 38:Mean values for K(ug/ml) in the leachates from the Spruce Grove, Cooking Lake and Ellerslie soil columns.

(values within soil types not underlain by similar letters are significantly different,P=.05)

		TREATMENT NUMBER				
SOIL TYPE	TIME (Months)	1	2	3	4	5
SPRUCE GROVE	2	8.3 c	3.4 c	1.9 c	1.7 c	1.3 c
	8	5.9 c	15.3 b	2.1 c	2.3 c	2.1 c
	11	5.8 c	27.2 a	3.9 c	3.2 c	1.6 c
COOKING LAKE	2	1.7 de	1.7 e	2.1 de	2.6 cde	1.5 e
	8	1.7 e	7.0 b	2.5 cde	2.3 cde	1.5 e
	10	1.7 e	9.6 a	3.1 cde	2.4 cde	1.5 e
ELLERSLIE	2	4.2 bc	5.0 bc	7.3 bc	6.7 bc	2.4 c
	8	5.2 bc	13.7 a	5.3 bc	5.3 bc	2.1 c

Appendix IX

Evidence for Enrichment of N-fixing *Spirillum* in the Tunnel Linings of *Lumbricus terrestris*

Table 39:ethylene produced from acetylene reduction by *Spirillum* enrichments from the tunnel linings of *Lumbricus terrestris.*

Soil Type	Replicate	um ethylene/24 hrs
Ellerslie	1	1.3
	2	1.2
	mean	1.2
Cooking Lake	1	14.5
	2	15.1
	mean	14.6
Spruce Grove	1	.7
	2	.6
	mean	.6

No ethylene was produced from control soil samples subjected to a similar assay.

Appendix X

Glossary of Micromorphological Terminology

Glossary of Micromorphological Terminology

(taken from Buckland,1983;Brewer,1976;Brewer and Pawluk,1975)

Crossed polarizers:A filtering arrangement where the orientation of two polarizing filters are such that the first orients light in a N/S direction and the second orients light in the E/W direction. When an object capable of rotating the plane of polarized light(e.g. clay minerals) is positioned between the filters the object is seen in a color characteristic of the orientation of the object with respect to the plane of polarized light.

Birefringence:The color of anisotropic minerals when using polarized light as viewed under cross nicols.

Skeletal Grains:grains larger than colloidal material which are comprised of indigenous minerals.

Plasma:colloidal sized, relatively soluble, organic and inorganic material which is not bound up by skeletal grains.

F-members:Recognizable entities that may be simple or compound but that occur as discrete units.

F-matrix:Grains of a size smaller than skeletal grains.

s-matrix:That material comprising primary peds, which may consist of plasma, skeletal grains and voids.

Related Distribution:the orientation of a group of like individuals with respect to a different group of like individuals. It can be described in terms of the relationship between plasma and skeletal grains or the relationship between matrix material and complex three-dimensional units.

The type of related distribution patterns observed herein include:

Porphyroskelic fabric:the plasma occurs as a dense groundmass within which skeletal grains are imbedded.

Granic Fabric Sequence:Unaccommodated, loosely packed, discrete units without coatings on or bridges between units. If the units exhibit some coalescence around the edges the term granoidic is used. Where the units are densely packed they may approach a porphyric type of fabric. Modifiers are typically added to describe the composition of the granic or granooidic units. They include ortho-(mineral grains), phyto-(partially decomposed plant fragments), humi-(highly decomposed, dark ,moder-like organic units), matri-(matrix material) and mull-(mull-like units consisting of plasma plus skeletal grains with plasma birefringence masked by organic matter).

Chlamydic Fabric Sequence:F-members are present as in the granic sequence but have matrix material wrapped around them as coatings. Coatings may be organic, clay, coarse grained or sesquioxides. The coatings may become so thick that they form bridges across grains(Plectic). Fabrics may also grade into porphyric types.

Fragmic Fabric Sequence:Relatively densely packed, accommodated discrete units without coatings, on, or bridges between units. A patterned appearance generally results due to separation of units by horizontal and vertical joint planes. When adjacent units appear partially united, the term fragmic is replaced by fragmoidic. Densely packed units of this fabric sequence may also approach the porphyric type. Modifiers may be used as in the granic fabric sequence.

Complex Fabrics:Designation of complex fabrics recognizes the presence of two or more modal fabric types within a given zone. They are recognized as mixed or separate.

Mixed Complex Fabrics:Fabrics in which the component fabrics are inextricably intermixed;that is, they are intimately associated with one another such that they connot be separated. An example is matri-mullgranoidic, in which mullgranoidic is dominant yet matrigranoidic material is found in intimate association.

Separated Complex Fabrics:The component modal fabrics can be separated into distinct, recurring zones. An example is mullgranic/mullgranoidic fabric where sharp boundaries exist between a dominant mullgranoidic fabric and subdominant zones of mullgranic fabric. A double slash(//) indicates there is a gradual boundary between the two fabrics.

Plasmic Fabrics:Analysis of the plasmic structure involves the description and classification of elements of the s-matrix, with particular reference to the distribution and orientation of clay domains. Optical properties, particularly extinction patterns, are viewed under crossed nicols and are classified according to : visible plasma crystals; the kind and degree of orientation of plasma grains; the kind and degree of preferred orientation; and the kind and degree of development of plasma separations. Plasmic fabrics observed herein fall into the sepic class of Brewer(1976), and have "recognizable anistropic domains with various patterns of preferred orientation".

Insepic fabric:striated plasma separations occur as isolated patches within a dominantly flecked plasma.

Mosepic fabric:striated plasma separations may adjoin each other but the appearance is otherwise flecked.

Vosepic fabric:a portion of the plasma separations are associated with the valls of voids, the remainder is flecked.

Skelsepic fabric:a portion of the plasma separations are associated with the surfaces of skeletal grains, the remainder is flecked.

Masepic fabric:elongated zones of striated plasma occur, the remainder is flecked.

Lattisepic fabric:plasma separations take on a lattice like pattern.

Omnisepic fabric:the whole field of view shows striated plasma separations.

Complex Plasma Fabrics:can be named where more than one plasma fabric is present. For example, if plasma separations are dominantly flecked with minor zones of oriented plasma occurring subcutanically in association with skeletal grains, the appropriate term is skel-insepic.

Voids:represent the pore fraction and are described with respect to their size, shape, smoothness and arrangement.

Shapes include:

Curved:acicular and planar voids that deviate significantly from a straight line or flat plane in the direction of their long axis.

Regular:there are no reentrant or acute angles between faces or segments of the walls.

Irregular:equant and prolate voids whose walls have a significantly irregular conformation.

Mammilate:where walls consist of rounded, interfering, spheroidal surfaces.

Descriptors for smoothness include:

Ortho:voids whose walls appear morphologically to be due to the unaltered, normal, random packing of plasma and skeletal grains.

Meta:voids whose walls appear morphologically to be significantly smoother than would result from the normal random packing of plasma and skeleton grains.

Packing voids:voids due to random packing of individuals.

Vughs:relatively large voids, other than packing voids, usually irregular and not normally interconnected with other voids of comparable size. Vughs may be so irregular and numerous that they intersect each other; these may be referred to as interconnected vughs.

Channels:voids that are significantly larger than those which would result from normal packing of single grains, and have a generally cylindrical shape.Descriptors for channels include:

arched:one relatively flat, planar surface compounded with an arc of a circle.

dendroidic:channels branch "after the manner of a tree", each branch having a downward trend but not necessarily vertical;there is no rejoining of branches.

trellised:channels branch and rejoin to form a regular network characterized by relatively long horizontal-to-subhorizontal channels interconnected by shorter vertical channels.

Planes:voids that are planar according to the ratios of their principal axes;by virtue of their shape and extent they constitute an obvious deviation from the normal packing of single plasma and skeletal grains.Planes are described according to the characteristics of their surfaces and include:

Joint planes:planar voids that traverse the soil material in some fairly regular pattern, such as parallel or subparallel sets.

Skew planes:planar,voids that traverse the soil material in an irregular manner, having no specific basis distribution or orientation pattern between individuals.

Craze planes:planar voids with a highly complex conformation of the walls due to the interconnection of numerous short flat and/or curved planes.

Pedological Features:Recognizable units within a soil material which are distinguishable from the associated material for any reason, such as origin, differences in concentration of some fraction of the plasma, or differences in arrangement of the constituents. Those observed herein include:

Cutan:A modification of the texture, structure, or fabric at natural surfaces in soil materials due to concentration of particular soil constituents or *in situ* modification of the plasma;cutans can be composed of any of the component substances of the soil material. Argillans are a specific kind of cutans composed dominantly of clay minerals.

Pedotubules:A pedological feature consisting of soil material and having a tubular external form, either single tubes or branching systems of tubes;its external boundaries are relatively sharp.Pedotubules described herein include:

Granotubules:composed essentially of skeleton grains without plasma or all the plasma occurs as pedological features.

Aggrotubules:composed of skeleton grains and plasma which occur essentially as recognizable aggregates within which there is no dirrectional arrangement with regard to external form.

Glaebule:A three dimensional unit within the s-matrix of the soil material, and usually approximately prolate to equant in shape. It is recognized either because of a greater concentration of some constituent and/or a difference in fabric compared with the enclosing soil material, or because it has a distinct boundary with the enclosing soil material. A nodule is a kind of glaebule characterized by an undifferentiated internal fabric.

Crystallaria:Single crystals, or arrangements of crystals of relatively pure fractions of the plasma that do not enclose the s-matrix of the soil material but form coherent masses.